

HUNTING OF BIRDS IN THE PERUVIAN AMAZON

By

Alfredo J. Begazo

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1999

TO CHRISTINE, RHEA, AND KATRINA

ACKNOWLEDGEMENTS

This study could not have been carried out without the help of numerous people. I thank members of my committee Dr. Richard Bodmer, Dr. Michael Moulton, Dr. Kathryn Sieving, Dr. George Tanner, and Dr. Douglas Levey for their advice and guidance. Special thanks go to Dr. Richard Bodmer for his assistance in every aspect of this dissertation.

The data collection was assisted by a number of people. I thank Rolando Aquino for helping with the collection of census data. Julio Curinuqui, Gilberto Asipali, Pablo Puertas, Cesar Reyes, Michael Valqui, and Richard Bodmer also contributed in significant ways in conducting the censuses. Etersit Peso conducted surveys in the markets in Iquitos. Jorge Beltran, Einer Vela, and Ramon Noa provided valuable field assistance. Their humor and patience to endure long stops along the trails, as well as, their ability to provide fresh fish was important.

I thank all households at the villages of San Pedro and Nueva Esperanza for their dedication in recording information required for this study. The Chistama family in Nueva Esperanza and Ruiz-Huanaquiri in San Pedro provided room and board while I was at the villages and made sure that there was food or at least masato left for me, regardless the time I returned to the household.

Other people also participated significantly in this dissertation. Juan Ruiz Macedoneo of Universidad Nacional de la Amazonia Peruana assisted with the identification of seeds in the stomach contents. Pablo Puertas shared his data and was

always willing to share his knowledge on hunting by ribereño people and other aspects of ribereño culture.

Logistical support was crucial in conducting this study. Access to remote unhunted areas was made possible through the invaluable support of Dr. Richard Bodmer and the crew of the “Nutria”. Doña Vilma, Julio Curinuqui, and Gilberto Asipali helped with food preparation, and trail cutting, and they shared their knowledge of the forest.

In Iquitos the home of Jose “Pepe” Alvarez and Elena Burga became the base of my constant travels and provided a sense of belonging during long stays away from home. The Hostal La Pascana and Doña Petty Sanati also provided a nice environment during my first trips to Iquitos.

I would like to extend my appreciation to people who influenced my decisions over time: First my parents for believing that whatever I did –even chasing birds around– was OK, as long as I was excited about it; my sister Suzy Begazo for her strong will and determination; Dr. John Fitzpatrick who was not involved directly in this study, but whose early influence played a significant role in my getting to this point.

My deepest gratitude goes to Christine Kelly for whom I could not count the ways in which she was such a key component in “us” getting a doctoral degree. Christine provided insight, maintained my focus, was patient during trying times, and continues to be a source of inspiration. Her cheerfulness and ability to help out in periods of great stress were essential to the completion of this study. Dawn Kelly was also very important in relieving me from household chores, especially during the writing process. My daughters Rhea, and Katrina wondered what I could possibly be doing in front of that

computer for so long when the sun was shining and when playing in the back yard was more fun. I thank my family for being there.

I thank the Biodiversity support program and the Chicago Zoological Society for their financial support. The Fundación Peruana para la Conservación de la Naturaleza also provided financial support for the initial phase of this project.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS.....	III
ABSTRACT.....	VIII
 CHAPTERS	
1 INTRODUCTION.....	1
Introduction	1
Overview.....	5
The Varzea and Upland Forests.....	5
Study Design.....	17
2 ECOLOGICAL VARIABILITY BETWEEN AND WITHIN UPLAND AND VARZEA FOREST.....	25
Introduction.....	25
Methods.....	27
Results.....	31
Discussion.....	38
3 DETERMINANTS OF BIRD HARVEST IN THE PERUVIAN AMAZON.....	45
Introduction.....	45
Methods	46
Results.....	56
Discussion	77
4 HUNTING AND POPULATION ABUNDANCE OF AMAZONIAN BIRDS.....	84
Introduction.....	84
Methods.....	85
Results.....	100
Discussion.....	113

5	ECOLOGICAL CORRELATES OF POPULATION DECLINE.....	121
	Introduction.....	121
	Methods	123
	Results.....	130
	Discussion	150
6	CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS.....	161
	Management recommendations.....	164
APPENDICES		
A	HUNTING DATA FORM.....	169
B	SAMPLE TRIADS OF THE LARGE-SIZED WILDLIFE CATEGORY.....	170
C	SAMPLE TRIADS OF THE SMALL-SIZED WILDLIFE CATEGORY.....	171
D	POPULATION DENSITY (INDIVIDUALS/KM ²) OF SPECIES IN UPLAND FOREST USING THE PROGRAM DISTANCE.....	172
E	POPULATION DENSITY (INDIVIDUALS/KM ²) OF SPECIES IN VARZEA FOREST USING THE PROGRAM DISTANCE.....	173
REFERENCES.....		174
BIOGRAPHICAL SKETCH.....		192

Abstract of Dissertation Presented to the Graduate School
Of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

HUNTING OF BIRDS IN THE PERUVIAN AMAZON

By

Alfredo J. Begazo

August 1999

Chairman: Dr. Richard E. Bodmer.

Major Department: Wildlife Ecology and Conservation

Bird hunting by ribereño people (rural Amazonians) in the Peruvian Amazon was studied in two of the most important Amazonian ecosystems; the upland and the varzea forests during May 1996 and February 1998. Upland and varzea forests are subject to different water regimes, which influence the ecology of wildlife and the activities of ribereño people. Birds are an important source of animal protein for ribereño people. However, the influence of hunting on bird populations in upland and varzea forests is unknown. The goal of this study were; to examine the association between hunting by humans and changes in population abundance of Amazonian birds; and to examine ecological traits associated with changes in population abundance from hunting. The objectives included the following: (1) to assess ecological variability between and within upland and varzea forests in terms of vegetation structure and availability of selected food resources, (2) to determine the harvest of birds in two villages established in upland and varzea forests, and discuss these harvests in terms of cultural and biological factors,

(3) to determine the influence of hunting on populations of Amazonian birds, and to evaluate the sustainability of current hunting in the two villages, and (4) to examine ecological traits associated with the ratio of change in population abundance between unhunted and hunted populations. Upland and varzea forests appear to differ ecologically between forest and within forest type. Results suggest that canopy and understory structure, and leaf litter cover differed between forest type, but were similar within forest types. Fruit abundance differed between sites sampled within upland and varzea forests. Village residents at San Pedro (SP) in the upland forest harvested a greater proportion of birds (669 birds of 29 species hunted by 115 people) than those at Nueva Esperanza (NE) in the varzea (955 birds of 24 hunted by 380 people). Hunters preferred large birds that had good quality of meat, such as the Cracidae (cracids), Tinamidae (tinamids), and Psophiidae (trumpeters), but the actual harvest indicated that hunters took what was available to them. Hunters took small and less preferred birds from the impacted fauna surrounding the settlements, and realized their preferences in areas less impacted, away from the settlements. Hunting appeared not to influence the populations Amazonian birds equally. Large cracids; *Mitu tuberosa*, *Penelope jacquacu*, *Pipile cumanensis*, and trumpeters; *Psophia leucoptera* showed the greatest ratio of population change between unhunted and hunted populations. Species of tinamous and *O. guttata* did not show significant changes in population abundance between unhunted and hunted populations. Changes in population abundance observed in all species were consistent in the upland and the varzea forests. Species of the Cracidae and the trumpeter appeared to be exposed to disproportional hunting pressure because of human preferences, naïve behaviors, and ease of detection. Hunters also prefer species of the

tinamous, but tinamous show secretive habits and efficient antipredator behaviors that appear to prevent overhunting of their populations. Changes in population abundance observed among species appear to have a biological explanation. Large cracids are preferred and easier to hunt, but are more vulnerable to population decline because of low intrinsic rates of population increases (r_{max}), long-lived individuals, and long generation times. In contrast the tinamous have high r_{max} , short-lived individuals and short generation times. Amazonian birds can be categorized in terms of their vulnerability to hunting using the correlations between cultural and biological factors described in this study. Recognizing bird populations' potential for harvest could help plan management strategies toward their sustainable use and their conservation.

CHAPTER 1 INTRODUCTION

Introduction

In Amazonia, hunting has taken place since prehistoric times (Perea 1995) and rarely caused local extinction because native Amazonians practiced nonselective and nomadic hunting in small groups (Dufour 1990). Recently, local extinctions from overhunting have become more common because forest-dwelling people have concentrated in sedentary settlements, adopted modern hunting technology and become involved in market economies (Robinson and Redford 1991, Padoch 1988, Stearman 1990). The association between hunting and patterns of population decline has been documented on primates (Peres 1990, Peres 1996b, Coltrane 1998), birds (Silva and Strahl 1991, O'Neil 1991, Mitchell and Racz-Luna 1991, Gonzales 1998), and ungulates (Peres 1996a, Bodmer et al. 1997) by comparing population abundance in areas of differing hunting intensities (Peres 1990, Glanz 1991). While most studies have concentrated on the immediate influence of hunting on population abundance, the reasons that some populations remain stable while others experience decline have been largely neglected.

After habitat destruction, overhunting is the second most common cause of recent extinctions (Atkinson 1989, Reid 1992). But extinction is rarely cataclysmic; rather, it is a progressive process with total extinction preceded by local extinction and local extinction preceded by population decline (Caughley and Gunn 1996). Hunting pressure

often leads to population decline because it removes reproducing individuals that result in lower productivity at the population level (Caughley 1977). Hunting pressure is potentially influenced by the abundance of wildlife available to hunters (Robinson and Redford 1986, Bodmer 1995b), hunters preference, spiritual and physiological prohibitions on the taking of certain species (Ross 1978, Ayres and Ayres 1991), hunting technology (Hames 1989), and ease of hunting (Fitzgibbon et al. 1996, Bengtson 1984). However, a given hunting pressure does not have similar implications on change in population abundance across species because species differ in their ability to compensate for individuals removed from the population (Robinson and Redford 1991, Bodmer et al. 1997, Fitzgibbon et al. 1996).

Few studies have addressed the implications of avian wildlife utilization among rural Amazonians. Mitchell and Rætz-Luna (1991) and Gonzales (1998) determined associations between hunting and population abundance of birds by comparing abundances observed in sites with differing intensities of hunting. Other studies quantified avian utilization by rural Amazonians to address the hypotheses of protein limitation (Gross 1975), hunting effort (Vickers 1980), ideas of taboos (Ross 1978), changes in hunting attitudes (Ayres et al. 1991), importance of wildlife for rural people (Gaviria 1981, Saravia 1992, Townsend 1995), and the effect of forest fragmentation (Cullen 1997). Most of these studies showed a clear bias towards including few of the large species (e.g., cracids and tinamous) while ignoring most of the smaller and less frequently hunted taxa in their analyses.

Most Amazonian ecosystems are inhabited by rural people known in the Peruvian Amazon as *riberños* or river people (FPCN 1994). Two of these ecosystems are upland

and varzea forests that make up most of western Amazonia (Malleux 1975) and are subject to differing seasonal riverine floods. Upland forests stand on areas of high ground and are not subject to riverine floods, whereas, varzea forests stand on low and flat terrain that is seasonally flooded for 2-4 months (Pires and Prance 1987). Differing flood regimes have significant implications on the plant community (Gentry 1988), population characteristics of mammalian wildlife (Emmons 1984, Peres 1996b, Bodmer et al. 1997) and the activities of ribereño people (FPCN 1994).

Addressing the implications of avian wildlife utilization by rural Amazonians is potentially important in promoting forest conservation. After small-scale agriculture, hunting is among the most important activities for ribereño people. But given the increasing human populations in sedentary settlements (Egoavil 1992), coupled with economic pressures (Padoch 1988), it is less and less likely that uncontrolled harvesting of wildlife is sustainable (Shaw 1991). To understand the influence that hunting has on avian wildlife, it is essential to determine how cultural and biological factors interact with ecological characteristics of Amazonian ecosystems. Identifying the reasons that lead to decline and those that lead to population stability can assist in developing general principles through which managers can direct their effort when addressing the use and conservation of Amazonian ecosystems.

In this dissertation, I examined the hunting of Amazonian birds and its association with their population abundances, as well as the proximate factors of population decline from hunting. I tested the hypotheses that hunting influence population of Amazonian birds and that species whose populations are influenced by hunting are ecologically different from others. The association between hunting and population abundance of

Amazonian birds was examined by comparing abundances observed in hunted and unhunted sites selected in varzea and upland forests. Habitat in each site within upland and varzea forest was assumed to be constant and population abundances similar among sites prior to hunting by humans. If hunting influences population abundance, I would predict that; one, rural Amazonians hunt birds in considerable number; two, population abundance in hunted sites be lower than those in unhunted sites. I first test the assumption that habitat within forest type are similar by quantifying the availability of food and forest structure in hunted and unhunted areas within upland and varzea forests. Then, I quantified the harvest of birds. Subsequently, I compared population abundances observed in sites with differing intensities of hunting and populations in unhunted or control sites.

Vulnerability to human hunters was tested by quantifying antipredator behavior assuming that the reactions performed by birds in response to my presence was similar to the reaction that birds would perform in the presence of an actual hunter. Species potential for population recovery from hunting was tested by obtaining species' reproductive parameters. Reproductive parameters obtained from captive-bred populations were assumed to be similar to those of wild populations. If there were traits that influence the vulnerability of some species to human hunters, I would predict that species that show these traits support a greater harvest pressure than others. If species differ in their potential for population recovery from hunting, I would predict that species that show greater potential for population recovery show a lower change in abundance between unhunted and hunted populations. I first tested whether species differ in their vulnerability to hunting by examining the harvest of birds in terms of the traits expected

to influence the species vulnerability to human hunters. Subsequently, I tested whether species differ in their potential for population recovery from hunting by examining reproductive parameters in terms of changes in population abundance between unhunted and hunted populations. Finally, I synthesized results and provided management recommendations.

Overview

The Varzea and Upland Forests

Varzea forest Varzea forest is defined as Amazonian forest subject to seasonal riverine floods. Varzea forests in Western Amazonia and the Peruvian Amazon are subject to periodic inundation for 2-4 months of the year (Kalliola and Puhakka 1993). Varzea forests occupy vast surfaces of mostly flat terrain that parallels major Amazonian rivers (floodplains). Varzea forest includes lakes, lagoons, levees, backswamps and, channel bars that vary in the length of inundation from permanent to temporary, depending on the geography of the terrain (Figure 1-1). The length of floods largely depends upon changes in water levels of major Amazonian rivers (Encarnación 1993).

Upland forest Upland forest is defined as forest not subject to periodic inundation. Upland forest stands on high ground (Pires and Prance 1987). Upland forest has been classified according to its physiography as a) terrace forest, with rolling hills up to 30 m of altitude, and slopes of 15-30%, and b) hilly forest, with hills of up to 180 m and slopes of 70-80% (Malleux 1975, Encarnación 1993).

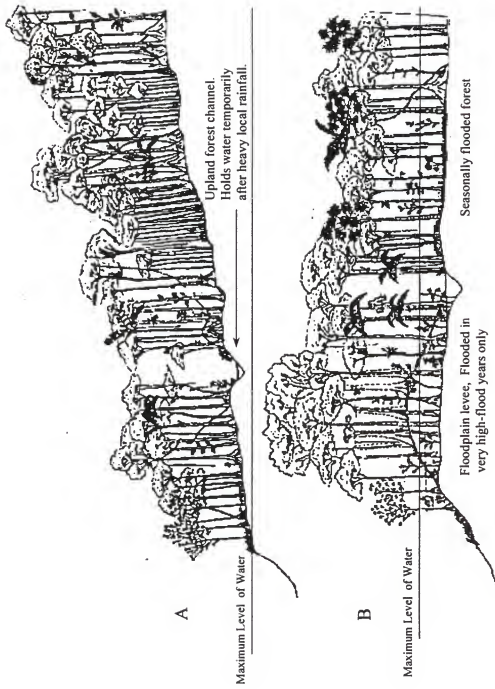


Figure 1-1. Typical cross section of (A) upland forest and (B) varzea forest.

Climate

The climate in the Peruvian Amazon is relatively uniform. The annual median temperature varies between 25.9°C and 26.8° C (Table 1-1). The fluctuation in temperature between day and night is greater than that between summer (March, the coolest month: 25°C) and winter (September-December, the warmer months: 27.4° - 26.9°) (Hueck 1978). On occasion, during the months of June and July, cold fronts from the south move to the region, causing the temperature to drop to 10°-5°C (Marengo 1984). Atmospheric humidity is nearly constant, varying from 80% to 100%.

Table 1-1. Data from weather stations in 5 cities in the Peruvian Amazon.

City	Altitude (m)	Location	Temperature (C°)			Annual Precipitation (mm)
			Median	Max.	Min.	
Iquitos	117	03°45"S, 73°12"W	25.9	15	35.5	2600
Yurimaguas	180	05°45"S, 76°05"W	26.8	11.3	37.8	1774
Pucallpa	148	08°25"S, 74°37"W	26.7	15.1	39.2	1399
Puerto Maldonado	256	12°35"S, 69°12"W	26	10	28	1423
Tarapoto	426	06°32"S, 76°19"W	25.9	11	38	1330

Source: Kalliola et al. 1993.

Changes in water level in the rivers and ultimately rainfall determine seasonality in the region. Months with high precipitation are called winter, while periods of low precipitation are called summer (Marengo 1984). However, rainfall at the regional level has little influence on the water level of rivers. Instead, climates in the Andean Mountain chain largely determine the fluctuation of water discharge in Western Amazonia (Kalliola

and Puhakka 1993). The maximum water discharge of rivers in the state of Loreto is recorded during the months of October-April (Kalliola and Puhakka 1993), and water levels in the rivers fluctuate between 2 and 15 meters (Dumont et al. 1990); (Figure 1-2).

Water Properties

Amazonian rivers are classified according to the physical and chemical properties of their waters. This classification is based on differences in suspension loads and tannin content. White-water rivers originate in the Andean Mountain chain (Sioli 1984), water has a large load of suspended sediments and is circum neutral in pH. Black-water rivers originates in water catchments in the lowland forest, water is low in suspended sediments and nutrients, but rich in humic substances and tannins. Black-water has an acid pH.

Vegetation

Rainfall and periodic floods influence nutrient availability and plant diversity of upland and varzea forests (Gentry 1988, Kapos et al. 1990). In upland forest, rainfall washes nutrients away, resulting in nutrient deficient soils (Encarnación 1993). On the other hand, seasonal floods from white water rivers replenish nutrient in varzea forest where nutrient availability appears not to be a limiting factor (Ayres 1993).

While soils in varzea forest are richer in nutrients, upland forest has greater botanical diversity. Gentry (1988) concluded that in a 0.1 ha plot surveyed near Iquitos (Perú), the number of plant species common to varzea and upland forest was very low. In the Ecuadorian Amazon, Balslev et al. (1987) listed 60 species (18%) common to adjacent upland and varzea forest of a total of 333 species recorded. Pires and Prance

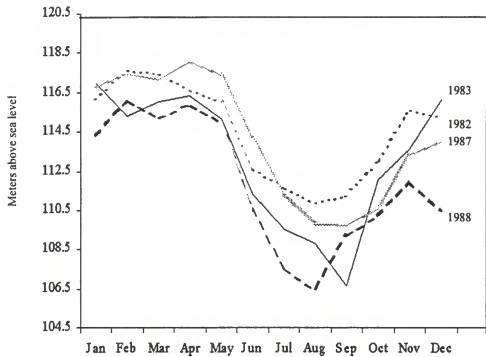


Figure 1-2. Seasonal fluctuation of the water level of the Amazon river. Data taken at the city of Iquitos, Instituto Nacional de Meteorología e Hidrología (from Kalliola et al. 1993).

(1987) also found similar results in a comparison of upland and varzea forest in the Brazilian Amazon. In overall terms, the richest ecosystems in plant diversity undoubtedly are in upland forest (Gentry 1992).

Plant distribution is more homogeneous in varzea than in upland forests. Because most plants in varzea forest rely on water and fish for dispersion (Goulding 1980), plants are usually more evenly dispersed. In contrast, topography and microclimate are associated with uneven distribution of plant species in upland forest (Hubbell and Foster 1986). Finally, topography, edaphic conditions, microclimate and hydrology were used to distinguish 7 plant communities in upland forest, and 9 in varzea (Encarnación 1993).

The People

The human population in rural Amazonia is composed of indigenous and mestizo people (mixed ethnic background) that are known in Peru as ribereños or river people (Egoavil 1992). The origin of the ribereños can be traced to the exploitation of the Peruvian Amazon during the 19th century. The transformation of Amazonian people from tribal groups to ribereños began with the earliest European immigration, and continued with the detribalization process imposed by missionaries, expansion of the slave trade, and influx of immigrants during the rubber boom. Due to the need for labor and the promise of prosperity, rubber exploitation attracted people from the Peruvian coast, the Andean region, Brazil, Europe, North America, Asia, and detribalized Amerindians (Dourojeanni 1990). Hence, the non-native population increased from 18,000 in 1876 to 120,000 in 1920 (San Roman 1975). After the abrupt ending of the rubber exploitation, many immigrants returned to their place of origin, but others

established themselves in the Peruvian Amazon where they turned their attention to other extractive activities (San Roman 1975).

Currently, ribereños greatly exceed indigenous people. Data from the 1981 census revealed that 280,000 nontribal people live in the rural sector of the state of Loreto, comprising 85 percent of the entire rural population. The remainder 5% are mainly indigenous people with a population of 50,000 (Egoavil 1992). Ribereño villages are located at the margins of major rivers and some are more than a century old (FPCN 1994). Indigenous groups and ribereños practice agriculture, fishing, hunting, small-scale lumber extraction, and collection of minor forest products. However, ribereños are more involved in market economies, in both the regional and international level, than are indigenous groups (Padoch 1988).

In the political arena, ribereños have been frequently forgotten or mistaken for colonists (rural Amazonians that emigrated from urban areas); (Padoch 1988). Human settlements in Amazonia are governed by local authorities and are, for the most part, recognized by the Peruvian government (FPCN 1994). Although ribereño villages outnumber those of indigenous people, studies on ribereño culture and their relationship with their natural environments have received little attention (Padoch 1988). Ribereños are the traditional, and in many cases, the exclusive users of many Amazonian environments, particularly the floodplains. Thus, the study and understanding of ribereños, and their use of resources, will enhance the possibilities of sound conservation policies for Amazonia.

The Birds

Twenty two species of birds from 9 orders and 13 families are treated in this study (Table 1-2). Species included in this study were reported taken by hunters in exploratory surveys in both human settlements. Four avian families occur only in the New World, and 89% of species are endemic to the humid lowland forest of Amazonia (Stotz et al. 1996). Species were classified in three size categories: small < 0.6 kg, medium > 0.6 – 1.5 kg, and large > 1.5 kg.

Hunting

Hunting is defined as the customary and traditional practice of procurement of wild animals for direct personal or family consumption as food and other non-edible by-products.

Background

The hunting of wild animals is important to the livelihood of rural Amazonians. Food (Dufour 1990, Alvard 1995), non-edible products (e.g., skins, hides, feathers) (Cajal 1988), and live animals (e. g., pets and biomedical research); (Inigo-Elias and Ramos 1991; Thomsen and Brautigan 1991) rank among the most important uses. Hunting of animals also is important for social reasons. For example, studies have shown that the type and amount of animals hunted is important to a hunter's prestige and the social cohesion of the family and village (Balee 1989, Stearman 1990).

Many studies on wildlife use have documented the harvest of birds among indigenous people in Amazonia. For the most part, anthropologists have included birds.

Table 1-2. Bird species included in this study.

English name	Order	Family	Genus	Species	Body mass (gr)	Altitude (m) ^a	Foraging strata	Habitat ^c
White-throated Tinamou	Tinamiformes	Tinamidae	<i>Tinamus</i>	<i>guttatus</i>	600	L - 850	T	Interior forest
Gray Tinamou	Tinamiformes	Tinamidae	<i>Tinamus</i>	<i>major</i>	1050	L - 1000	T	Interior forest
Bartlett's Tinamou	Tinamiformes	Tinamidae	<i>Crypturellus</i>	<i>bartletti</i>	241	L - 500	T	Interior forest
Cinereus Tinamou	Tinamiformes	Tinamidae	<i>Crypturellus</i>	<i>cinereus</i>	450	L - 700	T	Interior forest
Undulated Tinamou	Tinamiformes	Tinamidae	<i>Crypturellus</i>	<i>undulatus</i>	540	L - 900	T	Interior forest
Variegated Tinamou	Tinamiformes	Tinamidae	<i>Crypturellus</i>	<i>variegatus</i>	384	L - 900	T	Interior forest
Speckled Chachalaca	Galliformes	Cracidae	<i>Oriolus</i>	<i>guttata</i>	500	L - 1800	U/C	Interior forest
Spix's Guan	Galliformes	Cracidae	<i>Penelope</i>	<i>jacquacu</i>	1282	L - 1800	T/C	Interior forest
Blue-throated Piping Guan	Galliformes	Cracidae	<i>Pipile</i>	<i>cumanensis</i>	1425	L - 900	C/U	Interior forest
Wattled Curassow	Galliformes	Cracidae	<i>Crax</i>	<i>globulosa</i>	2500	0	T	Interior forest
Razor-billed Curassow	Galliformes	Cracidae	<i>Mitu</i>	<i>tuberosa</i>	3060	L - 900	T	Interior forest
Starred Woodquail	Galliformes	Phasianidae	<i>Odontophorus</i>	<i>stellatus</i>	310	L - 1050	T	Interior forest
Moscovy Duck	Anseriformes	Anatidae	<i>Cairina</i>	<i>moschata</i>	2468	L - 1000	W	Open habitats

Sources: Delacour and Amadon (1973), Hilty and Brown 1986, Dunning (1992), Stotz et al. (1996).

Table 1-2 continued

English name	Order	Family	Genus	Species	Body mass (gr)	Altitude (m) ^a	Foraging strata ^b	Habitat ^c
Toucans	Piciformes	Ramphastidae	<i>Ramphastos</i>	<i>spp</i> ^d	400	L - 1250	C	Open habitats
Amazonas	Psittaciformes	Psittacidae	<i>Amazona</i>	<i>spp</i> ^e	486	L - 1200	C	Open habitats
Macaws	Psittaciformes	Psittacidae	<i>Ara</i>	<i>spp</i> ^f	1130	L - 900	C	Open habitats
Gray-Fronted Dove	Columbiformes	Columbidae	<i>Leptotila</i>	<i>rufaxilla</i>	157	L - 1900	T	Interior forest
Pale-winged Trumpeter	Gruiformes	Psophiidae	<i>Psophia</i>	<i>leucoptera</i>	990	L - 1050	T	Interior forest
Neotropical Cormorant	Pelecaniformes	Phalacrocoracidae	<i>Phalacrocorax</i>	<i>brasiliensis</i>	2010	L - 3500	W	Open habitats
Anhinga	Pelecaniformes	Anhingidae	<i>Anhinga</i>	<i>anhinga</i>	1235	L - 900	W	Open habitats
White-necked Heron	Ciconiiformes	Ardeidae	<i>Ardea</i>	<i>coccy</i>	3200	L - 900	T/W	Open habitats
Boat-billed Heron	Ciconiiformes	Ardeidae	<i>Cochlearius</i>	<i>cochlearius</i>	656	L - 800	W	Open habitats

^a Altitudinal distribution where L= Lowland humid forest. Upper limits denote distribution into the Andean mountain chain.

^b Foraging strata where: C=forest canopy, T=terrestrial, U=forest understory, and W=water.

^c Species of open areas are those that typically inhabit the upper strata of the forest canopy or bodies of water.

^d Includes *Ramphastos cuculifer* and *R. cuculifer*.

^e Includes *Amazona farinosa* and *A. ochrocephala*.

^f Includes *Ara chloroptera*, *A. macao*, and *A. ararauna*.

in their analyses of wildlife use to test hypotheses of protein limitation (Gross 1975), efficiency of different weapons (Hames 1979), optimal foraging by humans (Hawkes et al. 1997), harvest per unit effort (Safirio and Hames 1983, Stearman 1990), ideas on taboos (Ross 1978), and various aspects of the use of wildlife (Rudle 1970, Yost and Kelley 1983, Townsend 1995). While ribereño people constitute the majority in the Amazonian rural sector, relatively little effort has been dedicated to the study of their use of wildlife (Smith 1976, Ayres et al. 1991). In the Peruvian Amazon, studies on uses of wildlife have focused on mammals (Bodmer 1990, Coltrane 1998), or have included birds only as a marginal component of their analyses (Saravia 1992, Gaviria 1981). Birds undoubtedly are important to the livelihood of rural people in Amazonia. Birds, especially the cracids (Cracidae) and tinamids (Tinamidae) ranged from 9.7% to 56% of all animals harvested in the most representative human groups in Amazonia (Ojasti 1993). However, little attention has been paid to the influence of hunting on populations of Amazonian birds and the factors that influence population decline from hunting.

Hunting of Amazonian wildlife typically causes a decrease in their population densities. This has been documented in mammals (Glanz 1991, Bodmer 1994a, Peres 1996b, Alvard et al. 1997, Coltrane 1998) and birds (Mitchell and Racz-Luna 1991). Hunting influences densities of wild populations located closer to human settlements more than than it does in areas distant from them (Mitchell and Racz-Luna 1991, Hill and Hawkes 1983, Stearman and Redford 1995). Furthermore, large primates (Peres 1990, Bodmer 1995b) and large birds (Cracidae and Tinamidae); (Dobson and Ortiz 1988, Mitchell and Racz-Luna 1991, Silva and Strahl 1991) seem to experience relatively greater rates of population reduction than other species.

While hunting typically reduces population size, natural variation in population density may influence the magnitude of the impact and survivorship of populations (Harper and Begon 1990). This is true because hunting would take a greater proportion of individuals from a small population than from a large population (Caughley 1977). Wildlife densities differ throughout Amazonia (Emmons 1984). Bodmer (1990) suggested that riverine floods in varzea forest explain the lower densities of ungulate species not adapted to semi-aquatic life. In contrast, riverine floods deposits nutrient rich sediments on soils in varzea forest, and rich soils in varzea forest have been used to explain greater mammalian (ground and arboreal dwelling species) biomass than in upland forest (Emmons 1984, Peres 1997).

Environmental characteristics of upland and varzea forest also has an influence on local people. Varzea forest has rich fisheries, and fish is the most important source of animal protein to local people (Gonzales 1998). In contrast, upland forest has small rivers that typically have smaller and less available fish (FPCN 1994). Moreover, soils in varzea forest have greater potential for agriculture than soils in upland forest (Dourojeanni 1990).

While some species experience population decline in response to anthropogenic disturbance, others maintain stable populations (Balmford 1996). Some species are preferred by hunters and vary in the extent that they are detected (Fitzgibbon et al 1996), and in the ease of hunting because they forage at different elevations within the vertical height of the forest, and perform antipredator behaviors that differ in efficiency to reduce the risk of human predation. These factors influence how often individuals of a species are taken by hunters. While greater hunting pressure often leads to population decline

(Caughley and Gunn 1996), species differ in their reproductive biology and the capacity to compensate for individuals removed from the population.

Birds have important ecological roles in Amazonia. Most species hunted by ribereños are frugivores and are important seed dispersers and seed predators (Janzen 1974, Terborgh 1986, Redford et al. 1992, Strahl and Grajal 1991). In addition, frugivorous birds have been found to contribute 60 to 70% of the total biomass of avian seed dispersers in most tropical bird communities (Janzen 1974, Terborgh 1986).

In the Peruvian Amazon, the government regulates the use of wildlife. Overhunting of species with valuable hides (e.g., some ungulates, otters and spotted cats), during 1950-1970, led to their dramatic population declines (Dourojeanni 1990). Consequently, in 1973 the Peruvian government prohibited commercial hunting in the Peruvian Amazon, and allowed hunting of a limited number of species for local consumption in the rural sector only (Decree: D. S. 934-73-AG). Legislation also curbed the harvest of commercially used species. However, hunting for local consumption remains largely unmanaged. While some groups in the Neotropics use wildlife at sustainable levels (Dufour 1990, Vickers 1991), there is evidence that other people hunt wildlife at levels that may not be sustainable (Alvard et al. 1997). Amazonian wildlife must be managed, but it poses a challenge given the complexity of Amazonian ecosystems (Freese 1997).

Study Design

A case study design was used to address the relationship comprising hunting and its influence on Amazonian birds. This natural experiment embodied two hunting

systems located in the major landscape characteristics (upland and varzea forest) and socio-economic features (riberño culture) of the Peruvian Amazon (Padoch 1988). This study examined the association between hunting and population abundance of Amazonian birds through a comparative observational design (Cook and Campbell 1979) involving populations subject to differing intensities of hunting and unhunted or control populations.

Research objectives

Hunting systems in upland and varzea forest offer an appropriate context in which to examine the hunting of Amazonian birds and its association with their population abundances, as well as the proximate factors of population decline from hunting. Bird species included in this study are mostly frugivorous, occur in upland and varzea forest, and use all dimensions of the forest (from the forest floor throughout the canopy). Additionally, upland and varzea forests are subject to differing environmental factors that influence characteristics of the forest (Hubbell and Foster 1983), ecology of wildlife (Emmons 1984, Peres 1996b, Bodmer 1990) and activities of local people (FPCN 1994).

The current study was designed specifically to test the relationships comprising hunting of birds and its association with population abundance, and the proximate reasons that influence population decline from hunting.

The overall research questions of this study are the following:

- 1.) Is hunting associated with changes in population abundance of Amazonian birds?
- 2.) Are species vulnerable to hunting ecologically different from others?

To test the hypothesis that hunting pressure influences populations of Amazonian birds, I

compared population abundances observed in sites with differing intensity of hunting with abundances in unhunted or control sites. If hunting influences populations of Amazonian birds, I would predict the following: one, ribereño people would harvest birds in considerable numbers; two, population size would covary with the intensities of hunting; three, population size of Amazonian birds would be lower in hunted than in unhunted sites.

Assumptions:

In testing these hypotheses I assumed that I controlled for habitat differences by choosing sites in upland and varzea forests. I also assumed that I controlled for intensity of hunting within upland and varzea forests by choosing sites that differed in intensity of hunting. Farther assumptions are that; one, the intensities of hunting in sites selected does vary as thought; two, population abundances in the sites with the differing intensities of hunting were similar prior to hunting by humans.

To test the hypothesis that species vulnerable to hunting are ecologically different from others, I examined whether species differed in traits that are associated to disproportional hunting pressure, and traits that influence their capacity to recover from individuals removed from the population. If hunting is associated to changes in population abundance, I would predict that; one, some species show traits that result in differential exposure to human hunters, and are hunted more often than others; and two, species differ in their capacity of recovery of individuals removed from the population, and show lower variation in population abundance between unhunted and hunted populations.

Assumptions

In testing whether some traits are associated with disproportional hunting pressure of some species, I quantified species antipredator behavior assuming that antipredator behavior performed by a bird in reaction to my presence would be the same as those they would perform in response to a true hunter. In testing whether species differ in their potential for recovery from harvest, I assumed that parameters obtained from captive-bred populations resemble those of wild populations.

Alternative Hypotheses

Hunting by humans may influence the populations of different species in different ways because of; one, differences in human population density, age of the human settlement, and settlement patterns between the hunting systems chosen in upland and varzea forest; two, preference of hunters; three, availability of alternative sources of animal protein that influence hunting pressure on birds; four, habitat modification in the surrounding of the human settlements that influence food base of certain species; and five, differences in population abundance between forest type.

I conducted fieldwork during 1996-1998. The results formed the basis for the chapters in this dissertation. In chapter 2, I discussed characteristics of upland and varzea forest ecosystems. I tested the hypothesis that:

- Upland and varzea forests differ ecologically between forest type, but are similar within forest type.

In this chapter, I discussed forest structure and abundance of food resources, as these ecological traits are likely to influence the occurrence and abundance of species. This discussion formed the basis for comparisons between harvest patterns, population

abundances, and the associations of hunting with population abundances.

In chapter 3, I discussed the harvest of birds, and the factors that influenced the harvest of birds. The specific questions answered were:

- Do hunters prefer some species of birds to others?
- Do hunters show similar hunting patterns between forest type?
- Are species hunted at the same intensity within and between forest type?
- Do search patterns influence the harvest patterns of birds?
- Are characteristics of the human settlement associated with harvest patterns of Amazonian birds?

This information on wildlife use formed the basis for examining the association between hunting with abundance of bird populations presented in chapter 4.

In chapter 4 I discussed the association between hunting and changes in population abundance. Subsequently, I evaluated the sustainability of hunting of Amazonian birds.

The specific questions answered were:

- Is hunting associated with variation in population abundance of Amazonian birds?
- Is current harvest of birds sustainable?

This information provided a measure of the association between hunting with populations of Amazonian birds.

In chapter 5, I discussed the reasons that some species were more susceptible to hunting than others. The specific questions answered were:

- Do species show traits that are associated with a disproportional vulnerability to human hunting?
- Do species differ in their capacity of population recovery from individuals removed from the population?

In chapter 6 I summarized the result of this study with respect to the association

between hunting and population abundance of Amazonian birds, and the factors that influence population decline from hunting. Finally, I provided management recommendations based on the results obtained in this study.

Study Area

The comparative method required adjacent sites that have areas hunted (=hunted areas), as well as areas with little or no hunting (=unhunted areas). The protected areas of Tamshiyacu-Tahuayo Communal Reserve (TTCR) located in upland forest, and Pacaya-Samiria National Reserve (PSNR) located in varzea forest, both in the state of Loreto, permitted this comparison. Areas within TTCR and PSNR were compared to hunted areas located in their periphery. Village residents of the village of San Pedro (SP) in TTCR hunted in areas within 25 km radius from the village whereas resident in Nueva Esperanza (NE) in PSNR hunted in areas within 18 km radius from the village. Areas within TTCR and PSNR were assumed to be subject to little or no hunting. This assumption is based on these sites being located in remote areas, and on their protected status. In upland forest, the center of the sampling activities at the unhunted area was located at S04°21'6.2', W71°51'04.9". The center of sampling activities at the hunted area was located at S04°20'14.3", W73°11'53". The centers of the hunted and the unhunted areas are separated by a distance of 135 km (Figure 1-3).

Site configuration in the varzea forest shows similar characteristics. The center of sampling activities in the unhunted area was located at S04°15'4.5" W75°49'30.9", and

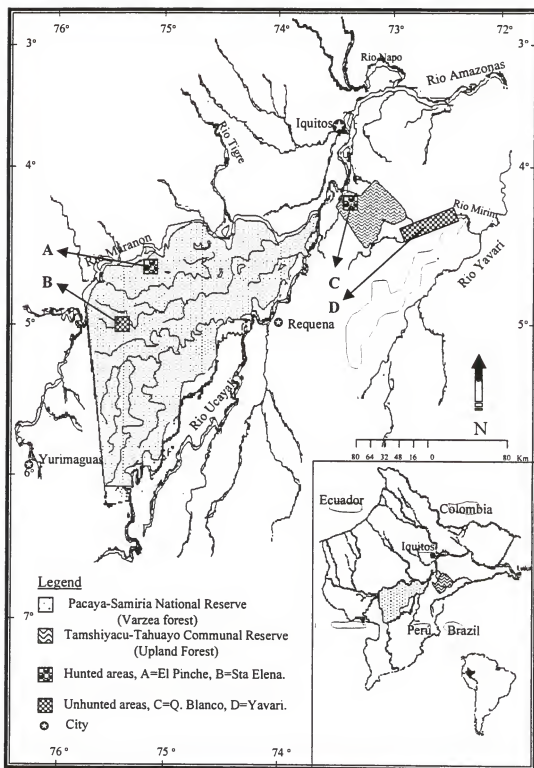


Figure 1-3. Map of the Pacaya-Samiria National Reserve and Tamshiyacu-Tahuayo Communal Reserve showing the location of the study sites.

the center of sampling activities at the hunted area was located at S05°51'13.3" W75°05'17.1". The centers of hunted and unhunted areas in varzea forest are separated by a distance of 43.4 km. Finally, there is a straight-line distance of approximately 230 km between the general areas sampled in upland and varzea forest. (Distances were estimated with a Geographic Positioning System (GPS).

PSNR encompasses 2,080,000 hectares of mostly flood prone forest (91.6%) and levees and terraces that escape inundation (6.5%); (Malleux 1975). PSNR lies within the Ucamara depression. The Ucamara depression encompasses 60,000,000 to 70,000,000 hectares of predominantly flat terrain that includes the confluence of the Marañon and Ucayali rivers at the point of origin of the Amazon River (Villarejo 1988). The Ucamara depression is seasonally flooded by nutrient-rich white water that flows from the Andean mountain chain (Sioli 1984). The geological history of the Ucamara depression reveals an active lateral movement of river courses that are still a prominent feature of the area (Kalliola and Puhakka 1993).

Upland forests in Western Amazonia are areas located in the lowland plateau of the lakebed that covered much of the Amazonian region in the Tertiary Period (Furch 1984). TTCR encompasses 322,500 hectares of mostly upland forest (71%) located on the terrace forest that divides the valleys of the Amazon from the valley of the Yavari rivers. Overall, the area corresponds to a type "a" (terrace) upland forest. In contrast to the varzea forest, upland forest represents an older and more static ecosystem. Soil formation has been dated to the Miocene epoch and shows deposits of elements of river systems that prevailed in past geologic periods. Thus, soils in upland forest are more weathered and relatively poor in nutrients (Sioli 1984).

CHAPTER 2 ECOLOGICAL VARIABILITY BETWEEN AND WITHIN UPLAND AND VARZEA FOREST

Introduction

Rich soils in varzea forest (Sioli 1984), have explained the greater biomass of nonvovoltant mammals (Emmons 1984) and primates (Peres 1997) than in upland forest. Conversely, the lack of tolerance to riverine floods have also explained the lower plant diversity in varzea than in upland forest (Gentry 1988). While upland and varzea forests show variation in some ecological traits, upland and varzea forest have been assumed to be ecologically similar within forest type (Bodmer et al. 1997, Coltrane 1998).

Animal biomass is largely dependent upon resources in the population's environment (Harper and Begon 1990). Variation in fruit abundance apparently influences frugivore abundance at the patch and local level (Levey 1988, Loiselle and Blake 1991, Blake and Loiselle 1991) and ecosystem level (Whitmore and Prance 1987). Fruit and invertebrates are the most important food resources for most Amazonian birds (Terborgh 1985, 1986).

Several factors may influence food abundance. Studies have documented that fruit abundance appears to be greater in lighted environments (Levey 1988, Loiselle and Blake 1991). Moreover, in Neotropical forest light passage through the canopy influences understory structure (Hubbel and Foster 1984). Edaphic characteristics (Kalliola et al. 1993) and plant community (Encarnacion 1993) may also influence the

variation in fruit abundance, patterns of fruit production, such as spatial distribution, size of fruit patches (by virtue of differing number of plant species producing fruit), and fruit size (Ayres 1993). Invertebrate biomass in the forest floor has been documented to be positively correlated with measures of leaf litter accumulations (Vitt and Zani 1998, Sweede 1998). However, the extent to which leaf litter accumulates may be influenced by differences in water regimes (Nadkarni 1994) between and within upland and varzea forest. Examining the mechanisms that are likely to influence the occurrence and abundance of animals is essential to interpreting life history traits, and, on the applied level, to interpret the implications of hunting by humans on population of Amazonian wildlife.

Most birds regularly hunted by rural Amazonians are frugivores (Redford et al. 1992). Up to 77.3% of species included in this study feed on fruit to varying degrees (Delacour and Amadon 1973, Strahl and Grajal 1991, this study). In addition, 71% of species that include fruit in their diets either forage exclusively (e.g., tinamous and trumpeters) or partially on the ground (e.g., cracids).

In this study, I tested the assumption that upland and varzea forests differ between forest type, but are ecologically similar within forest type. I tested this hypothesis in terms of variation in vegetation structure and food abundance between and within forest type. I first compared the canopy structure observed in selected sites within upland and varzea forests, as canopy structure determines light passage, which influences the structure (Hubbell and Foster 1986), and fruit production in the understory (Levey 1988, Blake et al. 1990). Sites sampled within forest type correspond to the unhunted and hunted sites from which most data for the chapters of this dissertation were obtained.

Then, I compared fruit abundance observed in sites within upland and varzea forests. Due to sampling constraints, I restricted the analysis of fruit abundance to a within forest comparison. Subsequently, I compared leaf litter accumulation observed in unhunted and hunted sites in both forest types as an indirect measure of abundance of invertebrates on the forest floor (Vitt 1998, Sweede 1998). I assumed the sites sampled had pristine plant communities and that variation in canopy structure, understory density and food abundance represented ecological differences that may influence the occurrence and abundance of animals (Pastor et al. 1997).

Methods

Sampling was conducted in “Q. blanco” (=hunted sites) and “Yavari” (=unhunted sites) areas in upland forest, and “El Pinche” (=hunted sites) and “Sta. Elena” (=unhunted sites) areas in varzea forest (Chapter 1). Vegetation structure, leaf litter cover, and fruit abundance were measured in 10 trails in upland forest and 12 trails in varzea forest (Table 2-1). To measure vegetation structure and leaf litter cover, I established sampling stations 500 m apart along freshly cut trails. To avoid bias from cutting, each sampling station was located at 5 m off the trail on the right hand-side regardless of the direction followed by the surveyor. If sampling on the right hand side was impossible due to physical circumstances, I proceeded on the left of the trail. Long and freshly cut trails were necessary because older trails tend to overestimate understory density and fruit production due to greater light availability. Furthermore, short trails tend to overestimate canopy fruit production due to the scale of the sample (See Blake et al. 1990).

Table 2-1. Sampling effort in sites in upland and varzea forest. Data on vegetation structure, leaf litter cover, and fruit abundance were obtained along the trails established in upland and varzea forests sites. Trails were surveyed only once.

Sampling sites	Number of trails per site ^a	Sampling stations per site	Readings taken at all sampling stations	Sampling schedule
Upland - Yavari	5	25	100	June 9 – June 30 - 1997
Upland - Q. Blanco	5	30	120	February 12 - 23 1997
Varzea - Sta. Elena	7	65	260	June 6 - June 17 -1996
Varzea - El Pinche	5	28	112	June 29 - July 14 - 1996

^a Each trail measured 4 km on average.

Light passage through the forest canopy influences understory structure (Hubbel and Foster 1986), and greater fruit production (Loiselle and Blake 1991, Levey 1988). To test whether this process differs between and within upland and varzea forest, I examined the structures of the forest canopy and the understory foliage in both forest types. To assess the percentage of canopy cover, I used a spherical densiometer (Lemmon 1956). I performed four readings rotating the densiometer in four opposite directions at each sampling station. Readings from equi-spaced dots on a concave grid correspond to the percentage of overhead area not occupied by canopy. The average of the four readings was multiplied by 1.04 and subtracted from 100 to obtain an estimate of canopy density in percent (Lemmon 1956).

To assess the understory foliage structure, I used a 2.13 m long pole graduated along its length. This pole was positioned vertically through the understory profile, and the number of foliage contacts within each 30.5 cm graduated section was recorded. This was repeated 4 times in four opposite directions at each point and an average foliage

contact-30.5cm was obtained. Foliage densities, that includes all plant species, was obtained for each of the 7, 30.5 cm height bands of the graduated pole.

To assess the leaf litter cover, I used a variation of the method used to measure foliage density (Bibby et al. 1992). The method consisted of looking at the ground through a 7.6 cm diameter and 20.3 cm long PVC tube. Then, I visually estimated the percentage that was covered by leaf litter. I made 4 measurements at each point and calculated the average leaf litter cover.

To quantify variation in fruit abundance within upland and varzea forests I used absolute counts of fruits. Because I attempted to document ecological variability within forest type, I also examined whether spatial distribution, path size (=aggregation of fruit of the same type) and fruit size varied between sites within forest type. The spatial distribution of fruit uses the time between encounters with a single fruit or fruit patch. This analysis assumed that variation in time elapsed between encounters with fruit indicated variation in spatial distribution of fruit.

To measure fruit abundance, I used a modification of an area-based survey (Blake et al. 1990) used by Hilty (1980). I counted all ripe and unripe fruit on the forest floor within 3 m on both sides of a trail, and those on shrubs and treelets within 5 m of height. All fresh fruit was counted regardless of condition (fresh, rotten, damaged or partially eaten). I did not distinguish between fruit produced by shrubs and treelets from those produced by the canopy (Janson 1983).

I obtained the time (minutes) elapsed between encounters with fruit at a speed of 1 km/hour. The size of fruit patch was obtained by counting the number of fruit of the same type at every encounter. When fruit of different types were found mixed in a single

aggregation, I recorded the number of each type of fruit and considered them as separate patches. An index of fruit size was obtained by taking two cross section measurements using a ruler. The approximation of fruit size uses the area (cm^2) obtained by multiplying the two cross-section measurements. To obtain the frequency distribution of fruit patch size and fruit size in sites within forest type, I indexed measurements obtained for patch and fruit size into size categories. The breadth of categories were determined on the basis of the range of measurements obtained for data on patch and fruit sizes.

Limitations of the Data Sets

There are several problems that must be considered in interpreting the data obtained during this study. Perhaps the most serious problem was the protocol used to obtain fruit data. In the varzea forest sites data on fruit was gathered in a period of 50 days allowing for comparison between sites. However, in the upland forest sites fruit data was gathered during June (least fruit production in north eastern Peru [Garber 1993], and February out of the period of least fruit production). This sampling problem likely bias the results toward greater abundance of fruit in the sites sampled out of the period of least fruit production. Characteristics of fruit (e.g., frequency distribution of fruit patch size and fruit size) are likely to be influenced by variation in sampling chronology. Variation in sampling protocol was largely due to logistic constraints.

A second problem was that fruit data from hunted sites may be influenced by both, the rarity or absence of large frugivores (e.g., large primates, ungulates, and large birds), and extractive activities by village residents. The unhunted sites are likely to have pristine animal communities and were free from human extractive activities (e. g., fruit

extraction, building material and lumber).

The results of the analysis of leaf litter cover should be interpreted considering the influence of seasonal floods on leaf litter cover. The analysis of leaf litter cover represents a point in time and observed differences may vary in function of the frequency and duration of seasonal floods in varzea forest, which are likely to influence leaf litter cover.

Results

Canopy cover and understory density. I examined the canopy structure as it influenced light passage to the understory and, thus, influenced understory foliage density and fruit production (Hubbel and Foster 1986, Levey 1988, Loiselle and Blake 1991). Percentage of canopy cover did not differ within sites in each forest type, and was nearly significant in favor of greater percentage of canopy cover in upland forest than in varzea forest ($P=0.1$) (Table 2-2). In upland forest, readings of percentage of canopy cover ranged within 10 points, while in varzea forest readings ranged within 21 points (each point represents approximately one percent of canopy cover [Lemmon 1956]). Thus, suggesting that the canopy in varzea forest is more variable in structure, and perhaps allows a greater passage of light to the understory layers than in upland forest (Table 2-3).

Foliage density, as measured by contact/30.5 cm, was significantly ($P=0.00$) higher in varzea (0.4 ± 0.46) than upland forest (0.28 ± 0.3) (Table 2-4). Layers differed in foliage density, but foliage density across the understory profile (=foliage density at each

Table 2-2. Summary statistics comparing canopy cover in upland and varzea forest. Data are the arc-sine transformed readings of percentage of canopy cover.

	Mean square	df	F	P
Between forest	0.02	1	2.75	0.1
Within sites	0.02	1	2.09	0.15
Forest type*Site	0.01	1	1.69	0.2

Table 2-3. Average percentage of canopy cover and minimum and maximum values obtained in sites within upland and varzea forests. Each measurement represents the average of four measurements taken at each sampling station along trails. Each trail measured 4 km on average and was sample one time.

Sampling sites	Canopy cover (%)	Range (%)
Upland - Yavari	87.3	81 - 92
Upland - Q. Blanco	87.4	83 - 92
Varzea - Sta. Elena	84.59	68 - 94
Varzea - El Pinche	75.83	77 - 93

Table 2-4. Summary statistics for the factorial ANOVA comparing understory profiles in upland and varzea forest. Data are number of foliage contacts/foot on a graduated pole.

	Mean Square	df	F	P
Between upland and varzea	2.51	1	17.80	0.00
Among layers	2.62	6	18.60	0.00
Between sites (within forest type)	0.01	1	0.05	0.82
Forest type * Layers	0.34	6	2.38	0.03
Forest type * Sites	0.00	1	0.03	0.86
Layers * Sites	0.09	6	0.62	0.71
Forest * Layers * Sites	0.17	6	1.20	0.30

of the seven height bands) did not differ within forest type ($P=0.82$) (Figure 2-1). The greater variability in canopy cover in varzea than in upland forest appears to support the contention that light passage influences the foliage density in the understory and perhaps influenced the greater understory foliage density observed in varzea forest.

Variation of fruit abundance within upland and varzea forest. I quantified fruit abundance within sites in upland and varzea forest by counting fallen fruit on the forest floor and fruit on shrubs and treelets. In varzea forest, fruit counted in "Sta. Elena" was greater than in "El Pinche" ($\chi^2=11.3$, $df=1$, $P=0.000$). Likewise, in upland forest fruit counted in "Q. Blanco" site was greater than in "Yavari" ($\chi^2=7.7$, $df=1$, $P=0.005$) (Figure 2-2). These results suggest that fruit abundance showed spatial variation within upland and varzea forest (Denslow et al. 1986). However, this results should be interpreted in terms of sampling schedules in upland and varzea forest.

Time (minutes) elapsed between encounters with fruit (single fruit or patch) was similar between "Yuracyacu" (3.1 ± 3.7) and "El Pinche" (3.4 ± 4.2) sites within varzea forest ($t=1.96$, $df=467$, $P=0.39$), but differed in "Yavari" (4 ± 4.3) and "Q. Blanco" (2.5 ± 2.5) in upland forest ($t=1.97$, $df=217$, $P=0.000$). While time elapsed within sites in varzea forest did not differ, variation in time elapsed between encounters in upland forest might be an artifact of the sampling during different months in "Q. Blanco" (Table 2-5).

I also examined whether fruit patch size differed within forest type. Variation in fruit patch size was assumed to reflect fruiting patterns within forest type. Small-sized fruit patches were predominant in sites within both forest types, and their frequency distribution did not differ between "Yavari" and "Q. Blanco" (Kolmogorov-Smirnov $Z=0.64$, $P=0.8$), and between "Yuracyacu" and "El Pinche" in varzea forest

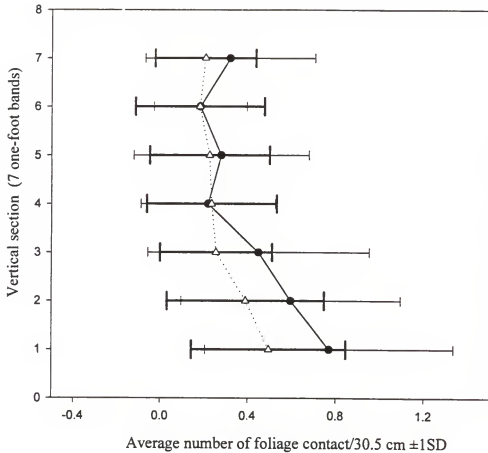


Figure 2-1. Understory foliage profile for upland (broken line) and varzea forest (solid line). The profile represents the average number of foliage contacts/30.5 cm on a graduated pole along the vertical section of the forest understory.

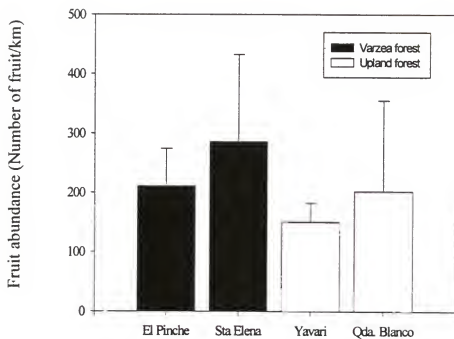


Figure 2-2. Variation of fruit abundance (Number of fruit counted/km). Bars (with error bars) represent fruit abundance recorded in 9 trail in varzea forest and 8 trails in upland forest. Trails averaged 4 km in length.

Table 2-5. Sampling effort and encounter rate of fruit in upland and varzea forest.

	Location	Distance surveyed (Km)	Total fruit counted	Mean encounter rate (minutes) ^a
Upland-Yavari	04 31'01.3"S 73 24'44"W	26.8	4014	4.02 ± 4.31*
Upland-Qda. Blanco	04 23'59.5"S 73 03'47.4"W	17	3439	2.45 ± 2.54*
Varzea-Sta. Elena	05 14'04.5"S 75 49'30.9"W	35.1	10,073	3.1 ± 3.71
Varzea-El Pinche	04 51'13.3"S 75 05'17.1"W	25.1	5,312	3.4 ± 4.16

* Significant at the 0.05 level.

^a Individual fruit or fruit patch encountered at an approximate pace of 30'/km

(Kolmogorov-Smirnov $Z=0.63$, $P=0.82$) (Figure 2-3).

I obtained fruit measurements to examine whether fruit size varied within upland and varzea forest. Small-sized fruit was predominant in both forest types and frequency distribution of fruit size categories was similar in the two sites within varzea forest (Kolmogorov-Smirnov $Z=0.42$, $P=0.99$), the two sites within upland forest (Kolmogorov-Smirnov, $Z=0.49$, $P=0.97$) (Figure 2-4).

Leaf litter cover. I examined the availability of invertebrates on the forest floor of both forest types by measuring leaf litter cover. This analysis assumes that greater concentrations of leaf litter reflect a greater invertebrate abundance on the forest floor (Sweede 1998). Upland forest had a greater leaf litter cover than varzea forest (Table 2-6). Leaf litter accumulation did not differ within forest type and ranges were similar (Table 2-7). This suggests that invertebrate abundance on the ground of upland forest might be greater than in varzea forest, but similar within forest type.

Table 2-6. Summary statistics comparing leaf litter cover. Data are the arc-sine transformed reading of percentage of leaf litter cover.

	Mean square	df	F	P
Between Forest	1.24	1	8.21	0.000
Within Sites	0.00	1	0.003	0.96
Forest*Site	0.00	1	0.002	0.96

Table 2-7. Average percentage of leaf litter cover and minimum and maximum values obtained in sites within upland and varzea forests. Each measurement represents the average of four measurements taken at each sampling station along trails. Each trail measured 4 km on average and was sample one time.

Sampling sites	Litter Cover (%)	Range (%)
Upland - Yavari	85.6	35 - 100
Upland - Q. Blanco	86	36 - 100
Varzea - Sta. Elena	75.83	21 - 100
Varzea - El Pinche	76.5	35 - 100

Discussion

Productivity of ecosystems dictates the potential to support animal biomass (May 1974). High productivity in the lowland Amazonian forest has often been used to explain its high biological diversity (Whitmore and Prance 1987). Nevertheless, the lowland Amazonian forest is composed of a myriad of ecosystems, some of which clearly differ in biological diversity and animal biomass (Tergorh 1992). Results of this study indicated that while vegetation structure and leaf litter cover varied between upland and varzea forest, fruit abundance also varied between sites sampled within forest type.

Varzea forest showed a more variable percentage of canopy cover. Wider range in percentage in canopy cover in varzea forest coupled with greater understory density suggests a greater passage of light than in upland forest. Klinge et al. (1990) suggested that seasonal floods in varzea forest are responsible for the low plant diversity and less complex canopy structure. Moreover, Encarnacion (1993), in a more descriptive study points out that the canopy of varzea forest is less dense and more heterogeneous than that

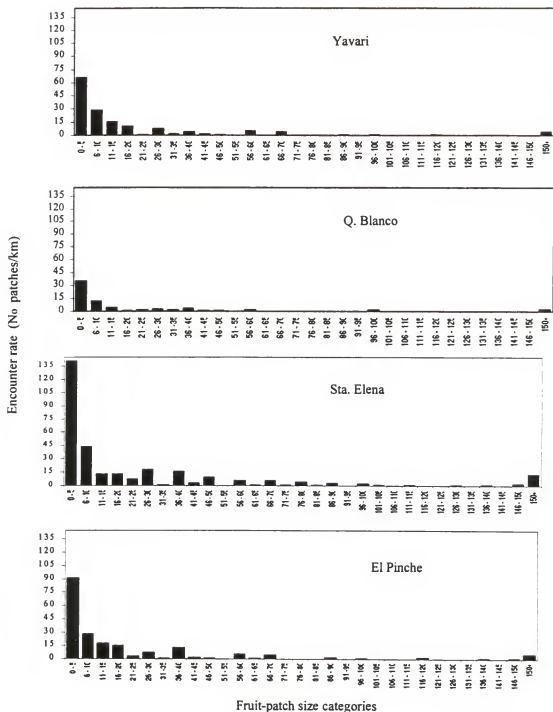


Figure 2-3. Frequency distribution of fruit patch/km. Data on fruit patch size was collected from a total of 9 trails in Yavari and Q. Blanco (upland forest) sites and a total of 8 trails in Yuracyacu and El Pinche sites (varzea forest). Trails measured 4 km on average.

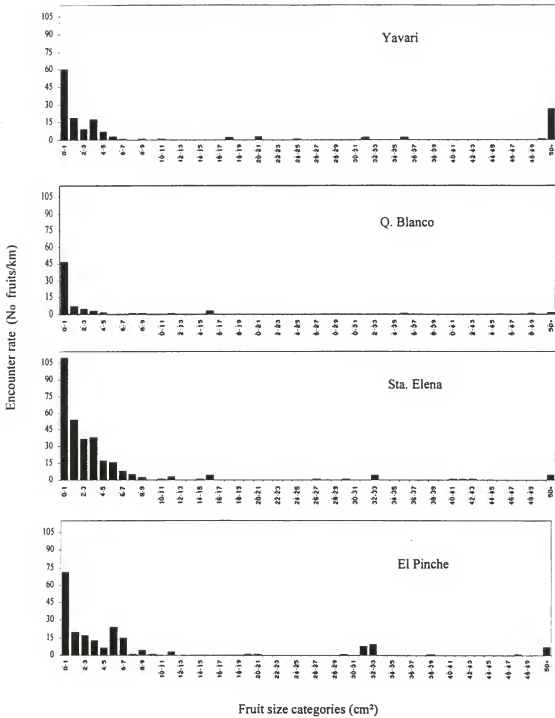


Figure 2-4. Frequency distribution of fruit patch/km. Data on fruit size was collected from a total of 9 trails in Yavari and Q. Blanco (upland forest) sites and a total of 8 trails in Yuracyacu and El Pinche sites (varzea forest). Trails measured 4 km on average.

of upland forest. Therefore, this suggests that upland and varzea forest differ in terms of canopy structure that may be partly responsible for greater foliage density in the understory (Hubbel and Foster 1986).

Failure to detect clear differences in canopy cover may have been influenced by sampling constraints in varzea forest. Due to access constraints, forest with permanent or near permanent water (e.g., swampy forest), that is often found in varzea forest, was circumvented. This type of forest has the lowest plant diversity and typically a broken canopy (Klinge et al. 1990). Most sampling in varzea forest took place in areas free from permanent water that supports plant communities that most resemble those in upland forest (Encarnacion 1993).

The spherical densiometer (Lemmon 1956) may not be an adequate device to compare canopy covers of high complexity. The quantification of the canopy cover relies on openings in the canopy that are mirrored in a concave grid. A common problem was that openings in the canopy were numerous but too small to meet the criteria needed to define a point of a percent, hence, leading to subjective approximations (Lemmon 1956). The lack of adequacy to assess cover in complex vegetation structures may derive from the fact that the spherical densiometer was developed and tested in less complex conditions of the tempered forest (for further discussion see Cook et al. 1995).

Fruit abundance varied between sites within forest type. Spatial variation in fruit abundance observed can be interpreted by linking documented pattern of phenology of fruit production in Neotropical forests and the sampling schedules used in this study. Sampling in varzea forest took place within a period of 50 days. Given the distance between sites sampled (43 km) it is likely that environmental factor influencing fruit

production (e.g., rain seasonality) in both sites were similar. Studies have documented relationships between variation of fruit abundance and habitat (Levey 1988, Loiselle and Blake 1991). While varzea forest is considered distinctive Amazonian forest ecosystem (Gentry 1988), there appear to be a myriad of plant communities within varzea forest (Encarnacion 1993) which could be influencing the spatial variation of fruit abundance. Moreover, fruit production may vary among individual trees of the same species (Wheelwright 1986), and in function to edaphic conditions (Kalliola et al 1993).

Fruit also varied in abundance between sites in upland forest. While factors discussed above also apply to upland forest, sampling schedule in upland forest may have influenced the results observed. The months of June-July are the period of least fruit production in northeastern Peru (Norconk 1986, Castro 1991, Garber 1993), and sampling in the "Yavari" site took place during June. While April-May constitute the peak of fruit production in the region, sampling in February may have constituted an artifact for the greater fruit abundance observed in "Q. Blanco" site.

Leaf litter cover was greater in upland forest than in varzea forest and suggests a greater abundance of invertebrates on the forest floor (Vitt and Zani 1998, Sweede 1998). Differences in leaf litter cover and in invertebrate biomass can be better understood by considering differences in seasonal floods between upland and varzea forest. Seasonal flooding of 2-4 months speeds the decomposition process (Vitousek 1985, Nadkarni 1994), washes away leaves, and likely kills most ground invertebrate fauna. Leaf accumulation in the flood-free upland forest is likely to provide better conditions to build up greater invertebrate fauna that favors at least the most terrestrial birds. Support for the influence of availability of insects on occurrence and abundance of wildlife stems from

the near absence of understory insectivore primates in varzea forest and greater abundance in upland forest (Peres 1997).

Environmental heterogeneity results in variation in resource abundance and influences the habitat's potential to support wildlife (Pastor et al. 1997). A greater light penetration through the canopy of varzea forest was linked to a greater understory density (Hubbel and Foster 1986) than in upland forest. However, fruit abundance was not uniform within upland and varzea forests. Differences in flood regimes between upland and varzea forest may also influence leaf litter accumulation and perhaps invertebrate abundance on the forest floor. Long periods of floods may result in a lower invertebrate biomass in the forest floor because water speeds leaf litter decomposition (Vitousek 1985), and washes away leaf litter cover. In addition, 2-4 months of inundation is likely to prevent formation of large invertebrate biomass on the forest floor.

Data indicates that structural characteristics of the canopy and understory as well as leaf litter cover appear to differ between forest type. However, fruit abundance differed between sites within forest type. These results support the assumption that upland and varzea forests differ ecologically. While structural characteristics of vegetation and leaf litter cover were similar between sites within forest type, fruit abundance varied. Variation in fruit abundance may influence frugivore abundance (Howe 1983, Levey 1988, Loiselle and Blake 1991) upland and varzea forests appear to vary ecologically within ecosystem and therefore population abundance, at least of the most frugivores species, may be influenced by ecological variation within each forest ecosystem. In conclusion, upland and varzea forests appear to show ecological variation within forest type, which may influence the occurrence and abundance of Amazonian

wildlife. This conclusion is considered in the study design and interpretation of results of subsequent chapters in this dissertation.

CHAPTER 3 DETERMINANTS OF BIRD HARVEST IN THE PERUVIAN AMAZON

Introduction

Anthropologists and wildlife biologists have collected data on hunting by humans to test a number of different hypotheses. Quantification of harvest of animals have been used to test hypotheses of sustainability of hunting (Townsend 1995, Fitzgibbon et al. 1996, Alvard et al. 1997, Bodmer 1997, Coltrane 1998, Begazo and Bodmer et al. 1997), hunting in habitats modified by humans (Jorgenson 1993), the efficiency of different weapons (Hames 1989, Alvard 1995), optimal foraging by humans (Hawkes et al. 1997), protein limitation (Gross 1975), cultural beliefs (Ross 1978), and socioeconomic importance of wildlife (Gaviria 1981, Saravia 1992, Pierret and Dourojeanni 1967). These studies generally reveal that hunters take a wide variety of animals at varying frequencies. However, the cultural and biological factors that determine the fauna available to hunters, and what ultimately they take have received little attention.

Wildlife available to hunters is the most obvious factor that may account for the type and quantity of animals hunted (Redford and Robinson 1987). What hunters take is also influenced by cultural factors, namely, hunter's preferences (Silva and Strahl 1991), cultural beliefs (Ayres et al. 1991, Ross 1978), economic incentive (Dourojeanni 1985, Bodmer 1995) and access to modern hunting technology (Vickers 1980, Vickers 1991, Yost and Kelley 1983). Cultural factors coupled with ecological characteristics of the habitat are likely to influence the availability of wildlife to hunters as well. For example,

settlement patterns, age of the settlement, human population density (Stearman and Redford 1995) and the extent of habitat modification in the surroundings of the settlements (Jorgenson 1993) influence the availability of wildlife and choices accessible to hunters.

Addressing the hunting pressure that species endure, and the factors that influence patterns of harvest are the first step in developing resource management in Amazonia (Posey et al. 1984). In an attempt to explore cultural and environmental correlates of the harvest of Amazonian birds, I gathered information on hunters' preference, hunting patterns, and harvest of birds from residents at four human settlements located in upland and varzea forests in North eastern Peru. I first determined the type and quantity of birds harvested in the human settlements. Then I examined the harvest in terms of hunter's preference, hunting patterns, and characteristics of the human settlements to ask whether the type and quantity of birds taken by hunters is associated with cultural factors. Subsequently, I examined the availability of other sources of animal protein (i.e., domestic animals and mammalian wildlife) in the settlements to explore whether hunting pressure on birds is associated with variation in the availability of alternative sources of animal protein.

Methods

Study Site

This study took place in the villages of San Pedro and Nueva Esperanza located in the buffer zones of PSNR and TTCR (Chapter 1). Data on hunting pressure also were obtained from the villages of San Felipe in Upland forest (W71°57'35", S4°18'06") and Dos de Mayo in varzea forest (W75°49'30.9", S05° 14'04.5"). Characteristic of the four

villages are provided in Table (3-1). Data were collected during May 1996 and February 1998.

San Pedro (SP) SP is located along the Blanco River, a tributary of the Tahuayo River, outside the area of influence of TTCR. The Blanco River is a typical upland forest watercourse that has high water levels only during the wet season (January-May), and maintains regular low water levels during the dry season (June-November). Residents of SP maintain commercial trade with the city of Iquitos. There is a straight-line distance of 74.8 km between Iquitos and SP and it takes approximately 8 hours by regular fluvial transportation to go between the two. SP can be considered a recent human settlement. Until the year 1990 only 7 households and approximately 35 people inhabited the area (P. Puertas personal communication). Since then, the human settlement has experienced an annual growth rate of 29% and population size has increased by 228%. The main activities are shifting cultivation, hunting, and fishing.

Nueva Esperanza (NE) NE is located on the periphery of PSNR, on the south bank of the Marañon River. The Marañon River constitutes a major commercial waterway connecting the Amazonian cities of Iquitos and Yurimaguas. The village is surrounded by a network of small waterways that are used by village residents to access the interior of the reserve. NE is an older village. Since about 1937, NE has been occupied with at least three households, whose main activity has been shifting cultivation, fishing, hunting and gathering (FPCN 1994). NE experienced an overall annual growth rate of 2.5% between the years of 1972-1992 (FPCN 1994).

Table 3-1. Composition of households and human population of villages sampled during 1996 – 1998 in upland and varzea forests. The harvest of birds is evaluated in terms of household sampled, hunters in households sample and consumers in household sampled.

Village	Forest type	Human population	Age of settlement	Settlement patterns	Habitat transformation	Households sampled	Hunters in households sampled ^a	Consumers in households sampled ^b
San Pedro	Upland	115	Approx. 15 years	Households spread in 28 km of meandering river.	Approximately 300 m radius	21	17	85
Nueva Esperanza	Varzea	380	Approx. 45 years	Households surround a central place.	Approximately 1000 m radius	57	33	165
San Felipe	Upland	91	- ^c	Households surround a central place.	- ^c	16	7	35
Dos de Mayo	Varzea	155	- ^c	Households surround a central place.	- ^c	28	19	125

^a Adult males that hunted regularly.

^b Hunters and non-hunters in the households. Includes (children and adult men and women).

^c Data not available for the village.

San Felipe (SF). SF is located on the Yavari-Mirim River which dissects vast areas of upland forest. Because of its remote location and difficult access due to low water in the river during half of the year (June-November) SF maintains limited commercial trade.

Dos de Mayo (DM) DM is located in a remote location on the Yuracyacu River and also maintains limited commercial trade with the city of Yurimaguas. DM lays in predominantly varzea forest within the limits of Pacaya-Samiria National reserve in the state of Loreto.

Recording Techniques

To obtain information about the specifics of bird hunting, I used a methodology that included participatory data collection, direct observation, and interviews. A diverse approach was necessary to corroborate information from village residents who were hesitant to provide information on their hunting activities. Although village residents in all four communities had previously worked with wildlife researchers, reluctance to cooperate was particularly noticeable in NE because most hunting took place within a legally protected area, and village residents showed some concern about the implications of this study.

The participatory method involved household members in the data collection. I interviewed all households in the villages and provided a booklet to households that voluntarily expressed interest in participating in this study. The booklets were provided during June 1996 and were kept by households for one year until July 1997. Booklets had the portraits and local names of the birds most frequently hunted (Appendix A).

Household members (e.g., adult men and women in a house) were asked to record; species identification; quantity; kill site; and date. The booklet-household method was supplemented with interviews with household members to account for birds not recorded on the booklets. When household members verbally reported a bird not registered in the booklets, I asked the same questions as for items listed on the booklets. Data on harvest yields were obtained from the participating households in each community (Table 3-1).

Direct observation and interviews also were used to gather data. I spent a total of 130 days in the village of NE and a total of 53 days in the village of SP. During these periods, I observed and accompanied hunting, fishing, and wild fruit gathering trips. I accompanied a total of 6 trips in NE and 4 trips in SP. In NE, 4 trips lasted less than a day and two up to 9 days in the hunting grounds. In SP, I was able to accompany only one trip of 6 days and the rest lasted less than a day. Participation on hunting trips were intended to observe the process of bird hunting. All hunting trips were part of hunter's regular activities, and were not undertaken under any request. Trips that I accompanied were with hunters from households that participated on the data collection through the booklet-household method. A hunting-gathering trip was defined as one intended to procure land animals, fish or forest products. In addition, household members were interviewed on the frequency, the duration, and species and numbers of animals taken during hunting-gathering trips, as well as, on the type and quantity of domestic animals kept by the household.

Composition of the Harvest

I obtained annual harvest of birds in each of the four communities by means of hunting records (booklet-household method) kept by household members. Information in booklets from the villages of NE and SP was transcribed to a permanent field data book approximately every 2 months. Booklets were transcribed and returned during approximately 1.5 hour-visit to participating households. A line separating transcribed from new records was drawn for each species after transcription. When space available for a species was filled out with records, I provided a new booklet. During the study, I provided 4 extra booklets to hunters that filled out the space of at least one species. Annual harvest from the remote villages was obtained from 7-month records kept by households in DM (November 1996 - May 1997), and 5 months in SF (February-June 1997).

Because the number of households sampled differed between SP and NE, I used harvest rates for comparative analyses (No. birds/consumer-year). Consumers are all household members over 5 years of age. I used consumer of 5 years and older to standardize the harvest per number of people that consumed to total harvest. This assumption implies that children less than 5 years of age did not consume the annual harvest at the same rate of consumers of 5 years and older. Consumption per consumer was used because birds are procured not only by adult male hunters, but also by other members of the households. In addition, households often supported multiple families. The annual avian weight harvested was obtained from the number of birds harvested multiplied by the species' body weight.

Hunting Technique and Access to Ammunition

Hunting technique is defined as the mean (e.g., hunting weapon, traps, fishing nets) used to procure birds. While transcribing data from the booklets to the permanent field notebook, I asked household members about the technique used to procure each of the birds. Direct observation was also used while accompanying hunting-gathering trips. Additionally, I asked about the price and mode to acquire ammunition. Information on the cost and access to ammunition was corroborated by obtaining the price and availability of ammunition at retailers established at the villages and from merchants traveling along rivers that stopped to commercialize goods at the villages.

Habitat Modification and Population Abundance

In this study, I examine two forms of habitat modification by humans; a) forest transformation to agricultural fields and their subsequent fallows, and b) palm trees and palm fruit extraction. Population abundance of some species increases in disturbed habitats (Posey et al 1984; but see Jorgenson 1993). However, the reduction of food resources that are important for a species is likely to influence their population abundance (Pastor et al. 1997). Based upon this premises, I analyzed stomach content samples of the species most frequently hunted, which included; the Cracidae (cracids), Tinamidae (tinamids) and Psophiidae (trumpeters) to examine whether habitat modification influences these species' diets, and possibly their population abundance and availability to hunters. Household members collected the stomach contents of birds that they hunted. They were previously trained on the preservation of stomach samples and supplied with material for their preservation. Stomach samples were preserved in a mix of 3:1

water/formaldehyde until the day of analysis.

Seeds found in the stomachs contents were identified to the species level when possible. Experienced botanists from a Peruvian University, “Universidad de la Amazonia Peruana”, aided with the seed identification. Using the frequency of plant species found in the stomachs, I obtained the percentage of occurrence of plant species. Additionally, I assessed the importance (volume) of three broadly defined food types; a) leaves, b) fruit (pulp and seed) and c) animal matter (invertebrates). I poured each stomach content into a 1.8-cm diameter dish, identified and sorted items, and visually estimated the relative wet volume of each of the three food types in each stomach sample. This analysis included taxa for which 10 or more stomachs were collected. Due to the small sample size, stomach samples collected in upland and varzea forest were pooled.

Importance of Birds

This analysis compares the annual avian harvest with the annual mammalian harvest recorded in NE (Bodmer et al. In Press) and SP (Puertas In preparation). Ribereño people typically sell part of the large species of ungulates and large rodents to the market and use small animals for household consumption (Padoch 1988). I examined the numerical importance and contribution in weight of birds in relation to that of mammalian wildlife harvested for household consumption.

Because economic incentive influences the type and quantity of wildlife hunted by ribereños (Dourojeanni 1985), I also examined if avian wildlife represented a source of income in the village and at the city market. The city of Iquitos’ two most important market places were visited every Saturday (the day of most commercial activity)

(Bendayán 1990). To account for the periods in which the commercialization of mammalian wildlife varied in magnitude (Bedayán 1980), sampling was conducted during the dry season (May through August 1997) and wet season (January through March 1997). Each visit consisted of inspecting the two market places for birds being offered for sale. Upon encounter I recorded species; sale price; number of individuals; and the condition (dead, alive, fresh or smoked). Because the commercialization of avian wildlife did not vary between dry and wet seasons, annual estimations were extrapolated from data obtained over 7 months.

Preference of Hunters

I examined hunters' preferences because hunters' perception of prey influences the type and quantity of animals taken (Ross 1987). Small mammals and birds are commonly consumed at households. To examine the possible influence of the availability and preference for alternative sources of animal protein on hunting pressure on birds, I quantify hunters' preferences of birds and mammals commonly used for household consumption. The rationale being that preference and availability of mammals commonly used for household consumption may influence hunting pressure on birds. Hunters' preference was determined through interviews using the method of triads (Bernard 1994). This method also has been called the "lie detector method", and it is an accurate and precise mode to determine an individual's position before an array of choices. The method consists of presenting the interviewee with "n" items randomly arranged in triplets that are shown one at a time. All possible triplets were randomized and presented to each interviewee one triplet at a time. The interviewees ranked the three

species presented on each triplet, and were asked to justify their choice. The number of triplets and the number of times that each item appears on the triplets are a function of the number of items included in the test. The results are based on the frequency that each item is ranked first by all interviewees. The preference for each species was obtained by dividing the frequency that each item was ranked first by the total number of interviewees.

Hunters' preference was determined in terms of characteristics (e.g., taboos on the consumption of certain species and palatability of the meat) of animals. Hunters prefer larger than smaller animals (Alvard et al. 1996). To remove the effect of size on hunter's choice, items were included in two separate tests on the basis of their similarity in body size. One test included 16 items; 8 mammals (average weight: 4 ± 1.7 kg) and 8 birds (average weight: 2 ± 0.8 kg), in 17 triads with each item appearing 3 times (see Bernard 1994) (Appendix B). The second test included smaller birds and mammals of similar size and included 14 items; 6 mammals (average weight: 0.9 ± 0.3 kg), and 8 birds (average weight: 0.7 ± 0.3 kg) (Appendix C).

Limitations of the Data Sets

There were several factors that must be considered when reviewing these results. One, these results were based on a small number of human settlements. As a consequence result could be biased toward specific characteristic of the human settlements studied and may not necessarily represent general patterns at the regional level. Two, the method of triads used to quantify preference tends to overestimate preference for species that interviewees are not very familiar with (e.g., rare species in

their hunting grounds) (Ross 1978). These factors may bias the results on hunters' preference because some species were not equally abundant in the hunting grounds of upland and varzea forest. Three, the quantification of annual harvest was based on voluntary participation of households. Because hunting is not equally important for all households within a human settlement, participating households may represent households for which hunting was an important activity. This sampling bias may lead to over estimation of the annual harvest of birds in the human settlements studied. Another factor that may lead to over representation of the annual harvest was that some household members appeared to be under the impression that I expected them to have the booklet with records at my bimonthly visits. This was noticeable in two households in NE that showed inflated numbers of curassows hunted in a period of two months. These records were not included in the study and I emphasized during my visits that the booklets were intended to keep records of birds that they would normally hunt. Four, annual harvests at the villages of SF and DM were extrapolated from 5 and 7 month records respectively. While annual harvest appeared to be similar throughout the year in the villages with complete annual records, there is the possibility that the harvest in the periods recorded vary from the harvest during the periods unrecorded in the two villages.

Results

Bird harvest. I recorded the avian harvests in four ribereño communities to determine preference, characteristics of the human settlements, hunting techniques, habitat modification, and access to ammunition. In the village of NE, a total of 955 birds were reported taken by 33 households or 165 consumers in a year period. This made up

an annual per consumer harvest of 6 birds or 6.6 kg-year. In the village of SP, a total of 669 birds were reported taken by 17 households or 85 consumers in a year period. This made up an annual per consumer harvest of 8 birds or 9.1 kg-year. Consumers in SP harvested a greater number of birds than in NE ($\chi^2=6.1$, $df=1$, $P=0.013$). Households in upland forest took a greater number of species (29) than those in varzea forest (24), ($\chi^2=7.9$, $df=1$, $P=0.004$) (Table 3-2).

Village residents at remote locations harvested a smaller number of species at lower per consumer rates than those at SP and NE (Table 3-2). In the village of DM, 142 birds were reported taken by 26 households or 125 consumers in a year period. This made up an annual per consumer harvest of 1.1 birds or 1.21 kg. In the village of SF, 112 birds were reported taken by 9 households or 35 consumers in a year period, which made up an annual per consumer harvest of 3.2 birds or 3.5 kg.

Preference. I examined hunters' preference to see how it influenced the avian harvest. In NE, 544 triads were presented to 33 hunters. Likewise, in SP 289 triads were presented to 17 hunters. In SP, hunters preferred mammals over birds (Kendall coefficient of concordance (KCC) $W=0.25$, $P=0.046$, $n=16$), whereas in NE, preferences were similar (KCC, $W=0.14$, $P=0.13$, $n=16$). Among wildlife of small size category, mammals were also preferred over birds in SP (KCC, $W=0.37$, $P=0.33$, $n=14$), and preferences were similar in NE forest (KCC, $W=0.14$, $P=0.16$, $n=14$). Hunters in NE regarded mammals and birds equally, and those in SP preferred mammals over birds. Silva and Strahl (1991), and Delacour and Amadon (1973) suggested that birds are heavily hunted because their meat is preferred over that of mammals. However, I did not find evidence to support this hypothesis among ribereño people in the Peruvian Amazon.

Preference of wildlife among ribereño people varied among individual households. Ribereño people represent a diverse ethnic group that is generally composed of village residents that have immigrated from other region within the Peruvian Amazon. This mixture of ethnic diversity and variation in costumes and was reflected in household' preference and the harvest of wildlife (Table 3-2). For example households that immigrated from indigenous groups showed a less specific preferences over species of wildlife. On the other hand, households of traditional ribereños showed a more selective preference over species of wildlife.

The distinction between household of indigenous descent and those of more traditional ribereño culture was also noticeable in terms of beliefs and taboos regarding the consumption of meat of certain species (Ross 1978). Households of indigenous descent considered beliefs and taboos in their hunting preferences, whereas modern ribereños did not consider beliefs and taboos, but the quality of the meat was more important in determining their preferences.

While hunters did not show differences in preferences between mammals and birds the bird meat was generally considered one of better flavor and with medicinal properties. Hunters indicated that meat from birds was often consumed in circumstances when hunters wished to eat meat of good flavor. Bird meat was also provided to people in the process of recovery from sickness or as specific medication for certain illness. For example, cracid meat was highly regarded as meat with medicinal purposes. Cracids were often requested by village residents as a form of medication for simple diseases or as a special nutritious food for women recovering from labor activities.

Table 3-2. Comparison of individuals hunted per species, percentage of total harvest, and per consumer harvest rate between the four villages studied.

Species	San Pedro			Nueva Esperanza			San Felipe			Dos de Mayo		
	Number of bird	Percent of total harvest	Harvest rate ^a	Number of bird	Percent of total harvest	Harvest rate ^a	Number of bird	Percent of total harvest	Harvest rate ^a	Number of bird	Percent of total harvest	Harvest rate ^a
<i>Tinamus guttatus</i>	28	4.2	0.33	-	-	-	-	-	-	-	-	-
<i>Tinamus major</i>	110	16.4	1.29	118	12.34	0.7	12	10.7	0.343	3	2.4	0.03
<i>Crypturellus cinereus</i>	-	-	-	34	3.56	0.2	-	-	-	3	2.4	0.03
<i>Crypturellus undulatus</i>	-	-	-	144	15.06	0.9	4	3.6	0.114	21	14.5	0.16
<i>Crypturellus variegatus</i>	4	0.6	0.05	-	-	-	-	-	-	-	-	-
<i>Crypturellus bartletti</i>	4	0.6	0.05	-	-	-	-	-	-	-	-	-
<i>Mitu tuberosa</i>	21	3.1	0.25	71	7.43	0.4	24	21.4	0.686	14	9.7	0.11
<i>Crax globulosa</i>	-	-	-	2	0.21	0.0	-	-	-	-	-	-
<i>Penelope jacquacu</i>	177	26.5	2.08	52	5.44	0.3	22	19.6	0.629	7	4.8	0.05
<i>Pipile pipile</i>	31	4.6	0.36	144	15.06	0.9	4	3.6	0.114	43	30.2	0.34
<i>Ortalis gutatta</i>	24	3.6	0.28	31	3.24	0.2	16	14.3	0.457	-	-	-
<i>Odontophorus stellatus</i>	2	0.3	0.02	-	-	-	-	-	-	-	-	-
<i>Cairina moschata</i>	5	0.7	0.06	22	2.30	0.1	2	1.8	0.057	2	1.2	0.01

Table 3-2. Continued

Species	San Pedro		Nueva Esperanza		San Felipe		Dos de Mayo	
	Number of bird	Percent of total harvest	Number of bird	Percent of total harvest	Number of bird	Percent of total harvest	Number of bird	Percent of total harvest
<i>Phalacrocorax olivaceus</i>	-	-	12	1.26	-	-	-	-
<i>Ramphastos spp</i>	33	4.9	25	2.62	2	1.8	-	-
<i>Amazona spp</i>	27	4.0	31	3.24	-	-	-	-
<i>Ara spp</i>	28	4.2	37	3.87	18	16.1	3	2.4
<i>Leptotila rufaxilla</i>	12	1.8	39	4.08	-	-	39	27.8
<i>Psophia leucoptera</i>	81	12.1	13	1.36	6	5.4	2	1.2
<i>Anhinga anhinga</i>	2	0.3	39	4.08	2	1.8	-	-
<i>Ardea cocoi</i>	24	3.6	21	2.20	-	-	-	-
<i>Cochlerius cochlerius</i>	4	0.6	72	7.53	-	-	-	-
<i>Ara manilata</i>	10	1.5	37	3.87	-	-	-	-
<i>Aratinga leucophthalma</i>	7	1.0	12	1.26	-	-	5	3.6
<i>Helornis fulica</i>	15	2.2	-	-	-	-	-	-
<i>Pionus menstruus</i>	17	2.5	-	-	-	-	-	-
<i>Morphus guianensis</i>	1	0.1	-	-	-	-	-	-
<i>Microastur ruficollis</i>	2	0.3	-	-	-	-	-	-

^a Total number of birds harvested divided by number of consumers at each village (Table 3-1).

All village residents from NE and SP justified their choices of wildlife on the basis of meat quality (smell and toughness) and the size of the animals (Figure 3-1). While animals within the large wildlife category differed in size (1.2 kg to 3.3kg), preference was independent of size in SP ($r=0.2$, $P=0.4$) or in NE ($r=-0.004$, $P=0.9$). It is widely agreed that size is the most important factor determining hunter preference (Redford et al. 1992, Alvard et al. 1997, Hawkes et al. 1997), but ribereño people appeared to compromise size for quality of meat, at least among the range of animals used in this test (Figure 3-1, 3-2).

Cracids, tinamous and trumpeters were consistently preferred in NE and SP, while herons, anhingas and cormorants, were less preferred. Preference for some species showed discrepancies between NE and SP. *M. tuberosa* was ranked among the top 6 species in NE but ranked lower in SP. Likewise *C. moschata* and *P. jacquacu* were ranked among the top 6 species in SP, but they were ranked lower in NE.

Finally, village residents in both forest types did not associate any spiritual or physiological prohibition on the hunt and consumption of any bird. They associated Night monkeys *Aotus nancymae* with reincarnated spirits. However, they hunted and consumed its meat, suggesting that traditional beliefs have little influence over the harvest of wildlife among ribereño people.

Overall, hunters appeared to realize their preferences. Cracids, tinamids, psittasids (parrots and macaws), and trumpeters (Psophiidae) were harvested at greater rates than species that did not meet characteristics of being large and having good meat (Figure 3-3). These results suggest that hunter preference influenced the type and quantity of birds taken and this is consistent in both SP and NE communities.

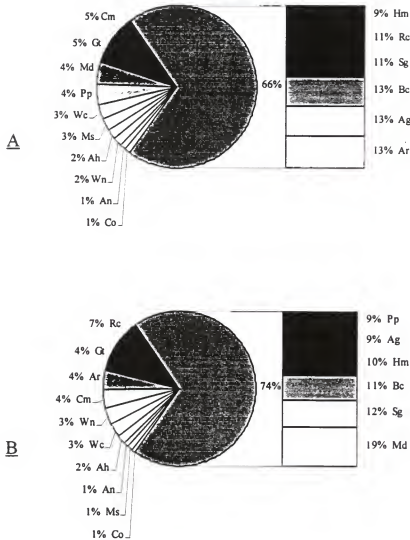


Figure 3-1. Wildlife preference obtained from village residents at A:San Pedro and B:Nueva Esperanza. Species belong to the large-sized category. Preference is given as the frequency (in percent) that each item was ranked first among the choices presented in the triads. Hunters' in upland and varzea forest show consistency in preference for mammalian species over avian species and cracids, and tinamous among avian species. Mammalian species are Wc=Cebus albifrons, Bc=Cebus apella, Hm=Alluata seniculus, Ms=Pythecia monachus, Ag=Dasypus fuliginosa, Ar=Dasypus novemcinctus, Cm=Nasua nasua, An=Tamandua tetradactyla. Bird species are, Gt=Tinamus major, Rc=Mitu tuberosa, Sg=Penelope jacquacu, Pp=Pipile cumanensis, Md=Cairina moschata, Co=Phalacrocorax olivaceus, An=Anhinga anhinga, Wn=Ardea cocoi.

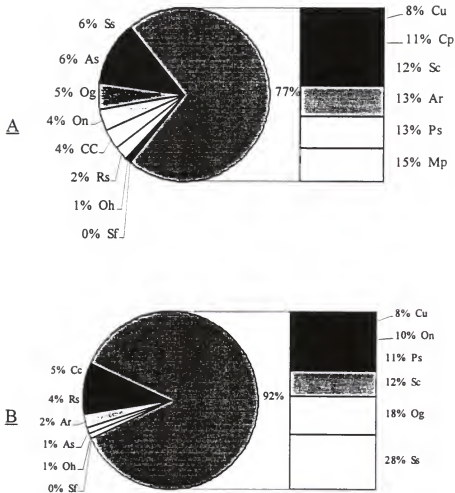


Figure 3-2. Wildlife preference obtained from village residents at A:San Pedro and B:Nueva Esperanza. Species belong to the small-sized category. Preference is given as the frequency (in percent) that each item was ranked first among the choices presented in the triads. Hunters in both forest types consistently preferred trumpeter over other avian species. Species are small birds and mammals where, Sf=Saguinus fuscicollis, On=Aotus nancymae, Sc=Saimiri sp., Cp=Callicebus cupreus, Mp=Myioprocta pratti, Ss=Sciurus spp. Cu=Crypturellus undulatus, Cc=Crypturellus cinereus, Og=Ortalis guttata, Oh=Opistocomus hoatzin, Rs=Ramphastos spp., As=Amazona spp., Ar=Ara spp., Ps=Psophia leucoptera.

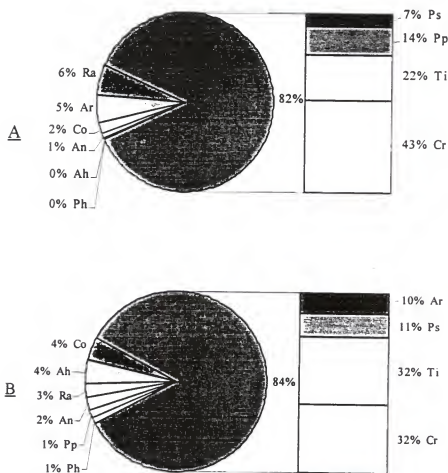


Figure 3-3. Percentage of avian meat (kg) harvested per household-year in terms of taxonomic group in **A**: upland forest, and **B**: varzea forest; where, Ti= Tinamidae, Cr=Cracidae, An=Anatidae, Ph=Phalacrocoridae, Ra=Ramphastidae, Ps=Psittacidae, Co=Columbidae, Ps=Psophiidae, Ah=Anhingidae, Ar=Ardeidae.

Hunting patterns. I examined hunting patterns of ribereño people, and characteristics of the human settlements in an attempt to find associations between the bird fauna available to hunters and what hunters took. Hunting birds was opportunistic and not mutually exclusive from other activities (e.g., fishing, gathering). Ribereños typically carried a shotgun on any outing, regardless of the purpose. Hence, birds were hunted upon casual encounters in the course of any activity and were regarded as the meat for the day's meal.

Birds were hunted in both short and long trips. A short trip consisted of searching for wildlife, fish, and forest products from the vicinity of the household to distances of approximately 5 km, and hunters returned to their household the same day. In SP short trips were undertaken by at least one member of the household ($n=17$ households), 1-5 times a week, with a mode of 2 and a weekly average of 3.05 times or 156.4 per year. In NE short trips were undertaken by at least one member of the household ($n=33$ households), 1-5 times a week, with a mode of 3, and a weekly average of 2.52 or 159 times per year. Frequency of short trips undertaken by hunters was similar in both villages ($t=2.02$, $df=40$, $P=0.13$). In SP short trips lasted 3.5 ± 1.8 hours while in NE 4.3 ± 2.6 hours ($t=2$, $df=48$, $P=0.21$). In both villages, short trips ranged wide in duration from short forays of 0.5 to 11 hours.

Long trips were undertaken less frequently. Long trips in NE took 2-15 days away from the household, with an average of 5 days. Long trips in SP took 3-11 days, with a longer average (7 days) than NE ($t=1.7$, $df=46$, $P=0.03$). Long trips in SP covered distances of up to 33 km with a mode of approximately 25 km, whereas in NE, long trips covered distances of up to 29 km with a mode of approximately 18 km. Hunters in NE

undertook a greater number of long trips per year (9.3 ± 6.1) than hunters in SP (4.6 ± 1.6) ($t=2$, $df=33$, $P=0.000$). Long trips in NE had fishing and hunting as the main objective whereas in SP hunting was the main objective.

Areas near the settlements were subject of a greater hunting pressure than areas away from the settlements. Residents in SP took more birds from areas near the settlement (short trips) (505) than from areas away from the settlements (long trips) (132), ($\chi^2=16$, $df=1$, $P=0.000$). Residents in NE took a similar number of birds from short trips (521) and from long trips (434) ($\chi^2=0.51$, $df=1$, $P=0.47$). Comparing short trips only, residents in SP took a greater number of birds than residents in NE ($\chi^2=4.4$, $df=1$, $P=0.04$), but both took a similar number of birds in long trips ($\chi^2=3$, $df=1$, $P=0.1$); (Table 3-3). Small and less preferred species predominated the take from short trips in both villages, and help explain their presence in harvest yields in spite of their low preference. In contrast, birds taken in long trips were predominantly large and preferred species, but account for a lower proportion of the total harvest (Figure 3-4).

The bird fauna surrounding NE differed in composition from that surrounding SP (Chapter 4). Variation in the composition of the bird community appears to be associated to differences in settlement patterns, a greater human population density and older age of NE than SP (Stearman and Redford 1993). The bird fauna available to hunters clearly influenced the take of birds from short trips in NE where hunters did not report the large cracids *M. tuberosa*, *P. jacquacu*, the trumpeter *Sophia leucoptera*, and only small numbers of *P. cumanensis*. The bird fauna in the surroundings of SP showed a more complete bird community (Chapter 4) and hunters reported taking all species from short hunting trips. This appears to suggest that characteristics of the human settlements,

Table 3-3. Number and percentage of birds hunted in short trips and long trips by hunters in San Pedro (upland forest) and in Nueva Esperanza (Varzea forest) during February 1997 through February 1998.

Species	Upland Forest				Varzea Forest			
	Short trips		Long trips		Short trips		Long trips	
	Number of birds	Percent of total	Number of birds	Percent of the total	Number of birds	Percent of total	Number of birds	Percent of the total
<i>Tinamus gutattus</i>	21	75	7	25	0	0	0	0
<i>Tinamus major</i>	94	85	16	15	74	63	44	37
<i>Crypturellus cinereus</i>	0	0	0	0	34	100	0	0
<i>Crypturellus undulatus</i>	0	0	0	0	138	96	6	4
<i>Crypturellus variegatus</i>	4	100	0	0	0	0	0	0
<i>Crypturellus bartletti</i>	4	100	0	0	0	0	0	0
<i>Mitu tuberosa</i>	6	29	15	71	0	0	71	100
<i>Crax globulosa</i>	0	0	0	0	0	0	2	100
<i>Penelope jacquacu</i>	131	74	46	26	0	0	52	100
<i>Pipile cumanensis</i>	9	29	22	71	9	6	135	94
<i>Ortalis gutatta</i>	23	96	1	4	27	87	4	13
<i>Odontophorus stellatus</i>	2	100	0	0	0	0	0	0
<i>Cairina moschata</i>	2	40	3	60	5	23	17	77
<i>Phalacrocorax olivaceus</i>	0	0	0	0	6	55	5	45
<i>Ramphastos spp</i>	33	100	0	0	21	84	4	16
<i>Amazona spp</i>	27	100	0	0	30	97	1	3
<i>Ara spp</i>	28	100	0	0	24	65	13	35
<i>Leptotila rufaxila</i>	12	100	0	0	39	100	0	0
<i>Psophia leucoptera</i>	54	67	27	33	0	0	13	100
<i>Anhinga anhinga</i>	2	100	0	0	22	56	17	44
<i>Ardea cocoi</i>	19	79	5	21	16	76	5	24
<i>Cochlerius cochlerius</i>	4	100	0	0	25	35	47	65
<i>Ara manilata</i>	10	100	0	0	37	100	0	0
<i>Aratinga leucophthalma</i>	7	100	0	0	12	100	0	0
<i>Helornis fulica</i>	15	100	0	0	0	0	0	0
<i>Pionus menstrus</i>	17	100	0	0	0	0	0	0
<i>Morphus gujanensis</i>	1	100	0	0	0	0	0	0
<i>Micrastur ruficollis</i>	2	100	0	0	0	0	0	0

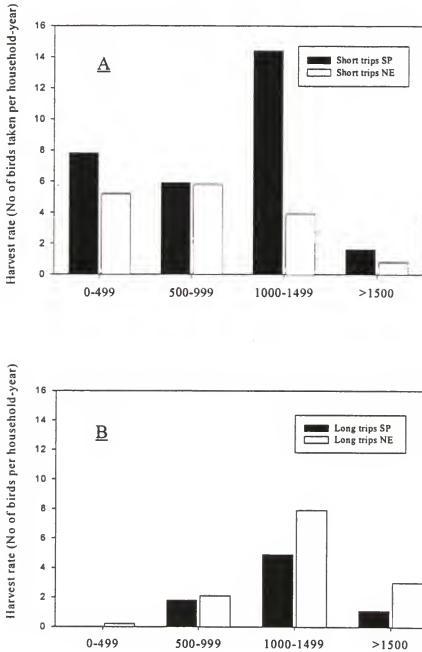


Figure 3-4. Size categories of birds taken in A short trips and B long trips. Small birds were taken at greater rates in short trips than in long trips. The cracid *Penelope jacquacu* still occur in the areas near SP and is hunted at high rates in SP and explains the high value in the 1000-1499 gr size category.

coupled with village residents' hunting pattern, may be associated to variation in the bird fauna available to hunters, which in turn appears to be associated to what hunters took.

The fauna available to hunters appeared to be influenced also by natural differences in abundance between upland and varzea forest. This was particularly evident in the hunting returns from long trips. *P. jacquacu* and *S. leucoptera* were more abundant in upland forest (Chapter 4) and hunters in SP took a greater number of individuals than in NE ($\chi^2=26.6$, $df=1$, $P=0.000$), ($\chi^2=36.1$, $df=1$, $P=0.000$). Likewise, *P. cumanensis* was more abundant in varzea forest and it was taken in greater numbers than in SP ($\chi^2=6$, $df=1$, $P=0.01$).

Access to ammunition and hunting technique. Access and cost of ammunition and the use of fishing nets influenced what hunters took. Hunter procured most birds with 16 gauge shotguns, and the harvest appeared to be influenced by the cost and access to ammunition. The price of a cartridge was greater (by 64%) in the remote villages of SF and DM (range \$ 1.6-1.9) than in NE and SP (range \$ 0.95-1.19). Households at SF and DM took half the number of species at lower average rates than those in NE and SP ($df=29$, $t=1.75$, $P=0.04$). Hunters unanimously declared that birds were hunted at low rates due to the high cost and difficult access to ammunition. These results concur with the notion that hunters in villages with easy access to hunting equipment are less concerned about the cost of ammunition and more likely to shoot a wider type and size of prey at greater rates (Vickers 1980).

The prevalence of fishing among residents in NE combined with high abundance of piscivorous birds resulted in a greater harvest of these species in NE than in SP. Only

2 anhingas and no cormorants were taken in SP. Although these species were not preferred 95% of anhingas taken in a year period (n=39 birds), and 40% of cormorants (n=12 birds) were accidentally trapped in fishing nets.

Baited cages, snares and fall traps were used in NE and SP to trap generally small birds (< 400 gr). Species captured with traps were the same in NE and SP (doves, wood-quails and small tinamous) and accounted for (7%) in NE and (5%) in SP of the total annual harvest.

Habitat modification. In this study, I examined two forms of habitat modification by humans; a) forest transformation to agricultural fields and their subsequent fallow, and b) palm trees and palm fruit extraction. Based on the premise that population abundance of some species increases in disturbed habitats (Posey et al 1984) and the reduction of food resources that are important for a species are likely to influence their population abundance (Pastor et al. 1997), I investigated the implications of habitat modification on the food base of Amazonian birds hunted by humans. Stomach samples of the *Tinamus* spp., *Crypturellus* spp., *O. guttata* contained mostly fruit, including plant species that typically grow in disturbed forest, human farming areas, and crops planted by humans (Figure 3-5). Stomach samples of *P. jacquacu*, and *P. cumanensis* showed mostly fruit of palms. The diet of *M. tuberosa*, and *P. leucoptera* consisted of fruit and insects, but did not show evidence of items that would be linked to habitat modification.

The frequency at which palm fruits occurred in the stomach samples of *P. cumanensis* and *P. jacquacu* was similar ($\chi^2=0.05$, $df=1$, $P=0.8$). The occurrence of palm

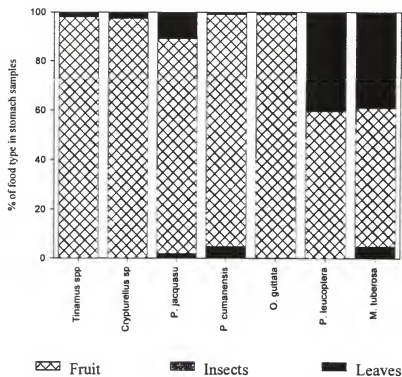


Figure 3-5. Proportion (percent volume) of food items identified from stomach contents of birds taken by ribereño people in upland and varzea forest. Stomach samples from upland and varzea forest were pooled to increase sample sizes as follows; *Tinamus spp.*= 29, *Crypturellus sp.*=31, *P. jacquacu*=36, *P. cumanensis*=20, *O. guttata*=10, *P. leucoptera*=19, and *M. tuberosa*=10.

species varied in the samples between species (Figure 3-6). However, all 6 palm species were heavily extracted for building material, food, and as a source of income (Vazquez and Gentry 1989).

Palm extraction is more prevalent near the settlements (personal observation), and it is likely that the older and more densely populated NE exerted a greater impact on palm trees than SP. In NE *P. jacquacu* has been locally extirpated while *P. cumanensis* is rare in the grounds used for short trips (Chapter 4). Conversely, the two species were regularly reported taken from the hunting grounds used for short trips in SP. While still exploratory, it is likely that differences in the availability of palm trees and palm fruit between the two human settlements influence the occurrence and abundance of species that depend on palm fruit in areas surrounding the human settlements.

In contrast, stomach samples of the Tinamidae revealed that their diet included species varied in the samples between species (Figure 3-6). However, all 6 palm species were heavily extracted for building material, food, and as a source of income (Vazquez and Gentry 1989).

Palm extraction is more prevalent near the settlements (personal observation), and it is likely that the older and more densely populated NE exerted a greater impact on palm trees than SP. In NE *P. jacquacu* has been locally extirpated while *P. cumanensis* is rare in the grounds used for short trips (Chapter 4). Conversely, the two species were regularly reported taken from the hunting grounds used for short trips in SP. While still exploratory, it is likely that differences in the availability of palm trees and palm fruit between the two human settlements influence the occurrence and abundance of species that depend on palm fruit in areas surrounding the human settlements.

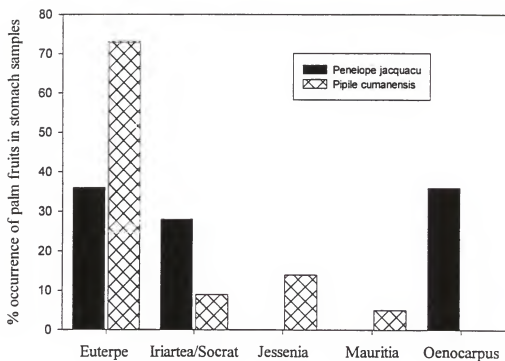


Figure 3-6. Occurrence of palm fruit in stomach samples of *P. jacquacu* and *P. cumanensis*. The percentage of occurrence of palm types varied between the two bird species but palms as a whole were found at similar frequencies in both species.

In contrast, stomach samples of the Tinamidae revealed that their diet included fruits and seeds of plant species that grow in secondary forest, as well as crops planted by human (Leopold 1959, Jorgenson 1993). Twenty nine percent ($n=58$) of stomach samples of *Crypturellus spp.* and *Tinamus spp.* combined, contained seeds of plants that are often found in secondary forest. Furthermore, 16% of the stomachs contained crops grown by people at the villages. Agricultural practices appear to provide supplemental food for these species of the tinamids. Greater availability of food often results in greater abundance of animals (Howe 1983, Loiselle and Blake 1993). Greater availability of food for *Crypturellus spp.* and *Tinamus spp.* in surrounding areas of the human settlements is likely to result in the greater population abundances observed (this study). Greater abundance of these species observed also reflects a greater representation in the harvest yields obtained by hunters.

Hunting pressure on birds. I examined the influence of alternative sources of animal protein on the hunting pressure of birds by measuring the availability of mammalian wildlife and domestic animals in SP and NE. I also tested the hypothesis that hunting pressure of birds is influenced by economic incentives by measuring the monetary value of birds.

Availability of mammalian wildlife. I examined the harvest of birds and mammals used for household consumption to see if differences in availability of mammalian wildlife influenced the hunting pressure on birds. In this analysis I assumed that SP and NE had equal access to ammunition, hunters did not prefer birds over mammals and that the harvest of small mammals represented availability. The later assumption is based on the hunting of animals for household consumption (e.g., birds and

small mammals) being largely opportunistic, reflecting the frequency of encounters between hunters and prey (Hawkes et al. 1987, this study). In SP, village residents harvested a greater number of birds than mammals used for household consumption ($\chi^2=13.6$, $df=1$, $P=0.2$). But avian weight in kg harvested was similar to the weight harvested for mammals ($\chi^2=0.2$, $df=1$, $P=0.9$). Likewise, in NE, hunters took a greater number of birds than mammals ($\chi^2=24.1$, $df=1$, $P=0.000$) and avian weight harvested was similar to the weight harvested from mammals ($\chi^2=0.14$, $df=1$, $P=0.71$) (Figure 3-7). Abundance of animals in the hunting grounds often reflects the harvest of wildlife among rural Amazonians (Bodmer 1996). Birds were hunted at similar rates as small mammals, suggesting that there is not variation in hunting pressure over one of the two groups, and this was consistent in both forest types.

Availability of domestic animals. People in SP harvested birds at greater rates than those in NE. I examined possible influence of meat from domestic animals on the hunting pressure on birds by measuring the prevalence of domestic animal in both villages. Animal husbandry was more prevalent in NE than in SP. In NE most households (92%) owned chickens, 38.9% ducks and 16% pigs. In SP 88.7% owned chickens, 2% ducks and 14% pigs. Domestic animals, especially chickens, were considered assets, and were frequently used as a source of income, as well as for household consumption (Gonzales 1988). In both NE and SP the proportion of households that owned chickens was similar. However, households in NE kept a greater number of chickens (16.4 ± 12.7) than household in SP (9 ± 6.1); ($t=2.63$, $df=39$, $P=0.006$). A greater potential for agriculture in the rich soils of varzea forest (Dourojeanni 1990) possibly influenced feed production and the potential

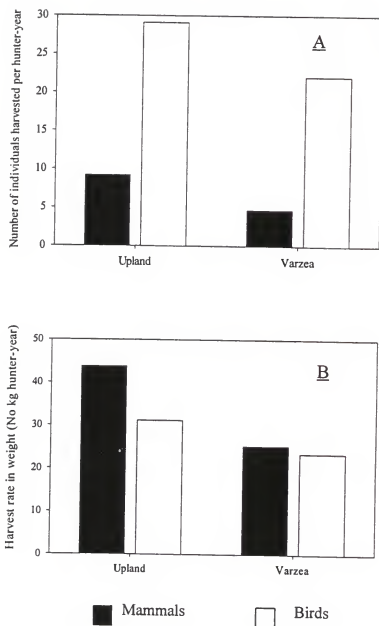


Figure 3-7. Comparison of A weight (kg) and B number of individuals between mammals used for household consumption and birds. Mammalian harvest was obtained from Bodmer et al (In Press) and P. Puertas (In preparation).

for domestic animal husbandry. This help explain the greater prevalence of domestic animals in NE than in SP. These results suggest that meat from domestic animals was more available in NE than in SP and may partly explain differences in hunting pressure on birds (Ayres et al. 1991).

Monetary value. I examined the magnitude of commercial trade of birds to see if monetary incentive was associated with hunting pressure on Amazonian birds. The city market study suggested that commercial use of species regularly hunted in rural areas was negligible (Table 3-4). A total of 21 species and 2791 individual birds was recorded in the two most important market places in Iquitos during a year period. Nearly half of the species commercialized in the Iquitos market (48%) were regularly used for consumption in SP and NE. However, species that were regularly hunted in the villages studied accounted for only 24 individuals or (0.9%) of the birds annually sold in the Iquitos market. Furthermore, most species consumed in the rural sector were sold as pets, and only 2 carcasses were offered for consumption.

Discussion

Studies on wildlife harvest reveal the wide range of species taken by Neotropical human hunters (Redford and Robinson 1987). Hunters usually prefer large-bodied animals to small-bodied animals (Redford 1992). This hunting preference makes economic sense since large-bodied animals provide more meat per cartridge. However, birds are an item used for household consumption often needed to obtain the meat for the day's meal, and cost-benefit relationships are not the most important reasons explaining

Table 3-4. Number of individual birds sold in the Iquitos market in a year period. Prices are in \$ US.

	Species	Condition of sale ^a	Number of birds	Price unit	Total value
<i>Tinamus major</i> *	Great tinamou	C	2	3.8	7
<i>Crypturellus undulatus</i> *	Undualted tinamou	C, L	2	2.4	4
<i>Mitu tuberosa</i> *	Razor-billed Curassow	L	2	7.1	12
<i>Penelope jacquacu</i> *	Penelope jacquacu	C, L	3	6.4	22
<i>Amazona amazonica</i> *	Orange-winged Amazon	L	3	26.2	90
<i>Amazona ochrocephala</i> *	Yellow-crowned Amazon	L	3	33.3	114
<i>Ara ararauna</i> *	Blue and Yellow Macaw	L	2	23.8	41
<i>Ramphastos sp</i> *	Toucans	L	2	7.1	12
<i>Psophia leucoptera</i> *	Pale-winged Trumpeter	L	2	14.3	24
<i>Ara severa</i> *	Red-bellied Macaw	L	3	7.1	24
<i>Aratinga leucophthalmus</i>	White-eyed Parakeet	C, L	346	0.5	160
<i>Brotogeris versicolorus</i>	Canary-winged Parakeet	C, L	1018	1.5	1520
<i>Pionus menstruus</i>	Blue-headed Parrot	L	5	5.1	26
<i>Veniliornis sp</i>	Woodpeckers	C	9	0.2	2
<i>Ardea cocoi</i> *	White-necked Heron	C	3	1.0	3
<i>Bubulcus ibis</i>	Cattle Egret	C	5	1.4	7
<i>Cacicus cela</i>	Yellow-rumped Cacique	C	17	0.6	10
<i>Tyrannus tyrannus</i>	Eastern Kingbird	C	298	0.1	43
<i>Tyrannus savana</i>	Fork-tailed Flycatcher	C	242	0.1	35
<i>Agelaius icterocephalus</i>	Yellow-hooded Blackbird	C	360	0.1	34
<i>Gymnomistax mexicanus</i>	Oriole Blackbird	C	463	0.2	85
	Total		2791		2276

^a Condition of sale C=dead fresh or smoked, L= Live animal, sold as pet.

* Species regularly hunted for subsistence purposes in the rural sector.

why hunters take what they do. Hunters preferred large birds with good quality meat, but their preferences were in proportion to the extent that birds were available to them. Bird availability is influenced by human population densities, settlement patterns, and age of the villages coupled with environmental pressures on bird populations. Additionally, the take of birds may be influenced by constraints in access to ammunition and by differential availability of alternative sources of animal protein. I have shown associations between factors that influence what hunters take and why they take what they do. However, factors are closely interrelated perhaps in an inextricable manner.

Characteristics of human settlements influence the composition of the fauna available to hunters. Large species of wildlife tend to become increasingly rare near villages, and the extent of rarification and local extinction is linked to the age of the settlement, number of hunters, and settlement patterns (Stearman and Redford 1995). These characteristics fit differences in the historic background of NE and SP, and explain the harvest composition obtained from short trips in both villages.

Differences in population abundance between upland and varzea forest influenced what hunters took. Species abundance varies among Amazonian ecosystems (Emmons 1984), perhaps in response to differences in availability of resources (Chapter 2). Among preferred species, greater abundance clearly reflected greater harvest in SP and NE. Greater abundance of less preferred species in varzea forest (herons, cormorants and anhingas) also resulted in greater representation in the harvest yields.

Habitat modification and extractive activities may influence the availability of birds to hunters. Agricultural gardens and disturbed forest have been associated with greater abundance of certain species of wildlife (Balee 1984, Denevan et al. 1984).

Moreover, Posey et al. (1984) argued that certain species would not occur in forest that were not modified by humans (but see Jorgenson (1993). Tinamous for example seem to take advantage of productive second growth and agricultural crops (Leopold 1959, Jorgenson 1993, this study), and were abundant and frequently hunted in areas surrounding of the human settlements.

Palm extraction is likely to have the opposite effect on species that depend on palm fruit. Palm fruit appears to be an important food resource for *P. jacquacu* and *P. cumanensis* given the wide spatial (upland and varzea forest) and temporal (18 months) sampling and the high percentage of occurrence of palm fruit in their stomach samples. Hence, the low availability of food areas surrounding the settlements, may help explain these species' absence and rarity and their little representation in harvest yields from short hunting trips.

The association between habitat transformation and palm extraction with variation in population abundance was consistent in SP and NE, and appeared to vary with the magnitude of the causal factors. NE is an older settlement and has a greater human population density than SP. Because palms used by cracids represent an important building material and source of income to ribereño people (Vazquez and Gentry 1989), it is likely that greater human population density in NE have exerted a greater impact on palm trees. While still exploratory given the nature of the evidence, bird populations appeared to correspond to hypothesized differences in habitat modification in NE and SP. Populations of the tinamous were greater in the hunted grounds of NE (Chapter 4) and were hunted more frequently than in SP. Conversely, *P. jacquacu* has been locally extirpated and *P. cumanensis* is rare in the hunting grounds near NE, while they still

persist and are taken from the grounds near the settlement in SP. Some village residents recognized the importance of palm trees for the cracids and deliberately left standing trees to attract them.

Hunting technique. Specific hunting techniques often determine the species and number of individuals taken by hunters (Hames 1980, Alvard 1995). Ribereño people in both forest types mostly used the same hunting technique but differed in the use of fishing nets. The use of fishing nets clearly influenced the greater harvest of diving birds in NE. However, it was more an ecological consequence rather than the use of a specific hunting technique given the opportunistic nature of taking birds with fishing nets (birds were accidentally entangled in fishing nets). Permanent bodies of water, fish and fish-eating birds are ubiquitous in varzea forest and people fish with nets more than in SP.

Data showed that high cost and limited access to ammunition led to low harvest rates of preferred species. Hunters in communities with access to ammunition near large cities are less concerned about the cost of ammunition (Vickers 1980) and more likely to take a wider range of birds including less preferred species and even small passerines. In remote communities where the cost and access to ammunition becomes more difficult birds were not considered a prey due to disproportional low return for the value of ammunition (personal observation). Hence, it can be generalized that communities located in areas where ammunition is readily available are more likely to exert a larger impact on bird populations. In addition the harvest of birds is characterized by the predominance of small and less preferred species. Other factors are also involved. Villages located in more accessible areas typically have greater human population densities and seem to have a greater impact on populations of Amazonian birds.

Intensity of the harvest. The harvest of birds was greater in SP than in NE. Gross (1975) suggested that the access of animal protein is perhaps the most important determinant of the number of individuals in a group, and nomadic movements among indigenous people in Amazonia. Other studies (Smith 1976, Ayres et al. 1991) have indicated that pressure over wildlife was relaxed in the presence of alternative sources of food (e. g., domestic animals, canned food). Birds and mammals used for household consumption were hunted at similar intensities and assumed to be equally available in both villages. But, domestic animals were more available in NE. Another, and perhaps the most important, difference that help explain the greater pressure over birds in SP is the access to fish. Varzea forest has rich fisheries (Bayley et al. 1992) and fish is a staple food in NE (Gonzales 1998). Basso (1973) pointed out that fish played an important role in the diet of indigenous people with access to this resource, to the extent that land animals were rarely hunted or considered low quality meat. In contrast lower availability of domestic animals and fish in upland forest ecosystems (Brack 1990) helped explain a greater hunting pressure on birds in SP.

Birds commonly hunted in both villages had little monetary value. In the Peruvian Amazon the sale of wildlife represents an importance source of income to ribereño people. However, birds did not represent a source of income and were entirely consumed at the household level indicating that unlike Amazonian ungulates, monetary incentive is not a factor influencing the harvest of Amazonian birds.

Conclusions

There are several factors that influence the type and amount of birds that ribereño hunters take. Overhunting associated with the age of the human settlement, human population density, settlement pattern and habitat degradation appear to influence the source fauna available to hunters. Hunters preferred some species to others, but their preference was realized to the extent of the availability of species largely due to consequences of history and characteristics of human settlements. The availability of species was also influenced by habitat differences between forest type, therefore, what hunters took. Cost and access to ammunition was also an important determinant of the type and quantity of birds taken. Differences in the type and quantity of birds taken in short and long trips provide an index of the impact that hunting has on populations of Amazonian birds. Finally, a greater access to fish, potential for agriculture and animal husbandry appear to reduce the need for animal protein for household consumption. This was observed in NE, whereas in SP limited access to these resources appears to result in a greater pressure over birds.

CHAPTER 4 HUNTING AND POPULATION ABUNDANCE OF AMAZONIAN BIRDS

Introduction

Wildlife in the humid lowland rain forest has traditionally been an essential source of protein for people (Dufour 1990). Despite significant cultural and socio-economic changes, hunting of forest wildlife is still an important activity that provides meat for household consumption and for the market (Dourojeanni 1985, Padoch 1988). However, wildlife resources are susceptible to overexploitation and species can be driven to local extinction.

Determining whether hunting in tropical forests is sustainable is difficult because one needs to understand the wildlife population status, the productivity of populations, the response of populations to hunting, and the extent of variation in patterns of hunting (Robinson and Redford 1991). These data are seldom available for rural communities or for tropical forest species. However, the need to evaluate the sustainability of hunting has resulted in the use of indices and models that provide a first evaluation of sustainability (Safirio and Hames 1983, Stearman 1990, Vicker 1991, Robinson and Redford 1991, Bodmer 1994). Models commonly used to evaluate sustainability of hunting rely on several assumptions sometimes derived from temperate species. Hence, evaluating sustainability of hunting have used several models intended to embrace the intricacies of natural systems and predict sustainability of hunting based on the consensus of results from the various models (Fitzgibbon et al. 1996, Coltrane 1998).

In this study, I examined the association between hunting and population abundance of Amazonian birds. The influence of hunting was inferred from comparisons of population abundances in hunted and unhunted (control) sites. I evaluated sustainability of hunting using models that rely on some knowledge of the biology of the harvested species, population densities, hunting pressure, and assumptions derived from studies of temperate species.

Methods

Sampling Design

This study evaluates the association between hunting and population abundance of Amazonian birds using a comparative observational design (Cook and Campbell 1979) involving two hunting systems. Each hunting system was composed of a human settlement, their hunting grounds, and distant areas within upland and varzea forest subject to no human hunting. One hunting system was located in and around the upland forest of the Tamshiyacu-Tahuayo Community Reserve (TTCR); (Figure 4-1), and the other in the varzea forest of Pacaya Samiria National Reserve (PSNR) (Figure 4-2). Within each hunting system, I compared population abundance observed in sites with differing hunting intensities; heavy, moderate, and light hunting with sites subject to no hunting (control). A site was defined as an area that represented an intensity of hunting. Sites were constituted by several sampling trails or line transects. Habitat was kept as constant as possible within the upland forest sites, and within the varzea forest sites. This assumption is based on the sites being located in continuous upland and varzea forest not separated by any major barrier (e.g., a major Amazonian river), similar plant

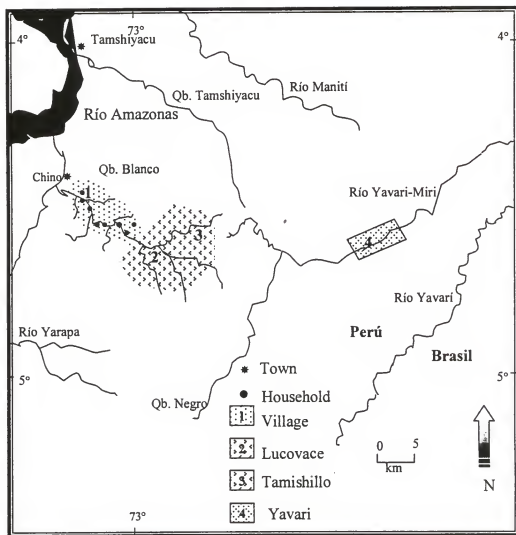


Figure 4-1. Map of the area sampled in upland forest showing the sites with the three intensities of hunting, 1=Heavy, 2=Moderate, 3=Light and the control 4. The study area in upland forest is located within Tamshiyacu-Tahuayo Communal Reserve in the state of Loreto, Northeastern Peru.

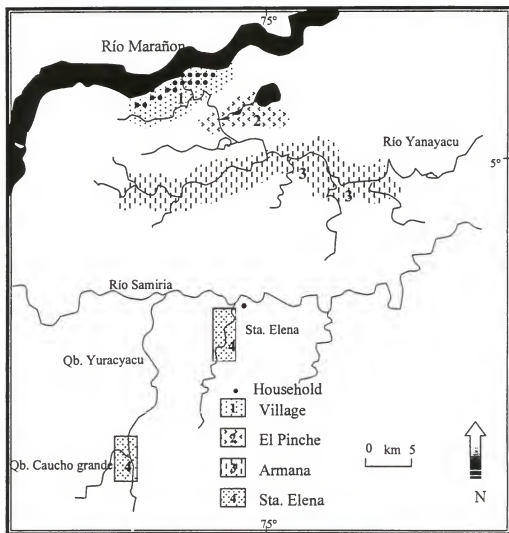


Figure 4-2. Map of the area sampled in varzea forest showing the sites with the three intensities of hunting, 1=Heavy, 2=Moderate, 3=Light and the control 4. The study area in varzea forest is located within Pacaya-Samiria National Reserve in the state of Loreto, Northeastern Peru.

(Encarnación 1993) and wildlife communities. Sites with differing intensities of hunting were chosen on the basis of both, the distance between sites and human settlements, and hunting intensity at these sites. Hunting intensity was determined from interviews with hunters on the frequency of hunting trips to these sites (Table 4-1).

Table 4-1. Sites with differing intensities of hunting in upland and varzea forest. Distances are straight lines connecting the village with the sites sampled. Annual frequency is the percentage of trips to the area sampled. Village residents provided annual frequency of trips.

	Nueva Esperanza (Varzea)		San Pedro (Upland) ¹	
	Distance (km)	Annual frequency (%)	Distance (Km)	Annual frequency (%)
Heavy (1)*	4.5	41	3	50
Moderate (2)	14	18	18	25
Light (3)	22	9	26	25
Unhunted (4)	43.3	0	135	0

(*) Number in parenthesis identifies the location of sites on the map.

(1) (P. Puertas In preparation).

The comparison between hunted and unhunted sites was conducted in the protected areas of TTCR in upland forest, and PSNR in varzea forest, both in the state of Loreto. Areas within TTCR and PSNR were compared to hunted areas located in their periphery, near the human settlements of Nueva Esperanza (NE) and San Pedro (SP). In upland forest, the centers of the hunted sites and the unhunted control are separated by a distance of 135 km. In varzea forest, the centers of hunted and unhunted areas were separated by a distance of 43.4 km. Finally, the areas that encompassed all sites within upland forest and all sites within varzea forest was separated by a distance of 230 km. Distances were estimated with a geographic positioning system (GPS, Garmin 12XL).

After determining the association between the intensity of hunting and patterns of population change from site to site, I determined the sustainability of hunting. The evaluation of the sustainability of hunting uses population densities obtained in unhunted sites within each forest type and pooled data from hunted sites with the differing intensities of hunting within forest type.

Relative Abundance and Population Density

I measured abundance as the number of individuals sighted per 100 km of line transects surveyed. Trails were cut in a predetermined direction using a compass, and were located along rivers, usually within 1.5-2 km from each other. Birds were censused by walking a trail at an approximate speed of 1 km/hour. I first recorded the species and the number of individuals per sighting, then proceeded to tape measure the perpendicular distance between the trail and the initial position of the animal. When a group of animals was sighted, I measured the perpendicular distance between the trail and the center of the group at its initial position.

A total of 28 line transects that made up 113 km were opened in upland forest. Likewise, a total of 24 line transects that made up 102 km were opened in varzea forest. Line transects averaged 4 km in length. Censuses were conducted between the 0700-1530 hours. Each line transect was censused once per day and up to 6 times after opening.

To census water birds, I also conducted censuses along sections of rivers and small tributaries by means of dugout canoes powered by paddles and/or small outboard motors. A total of 9 separate sections of rivers and tributaries were censused in upland

forest. Likewise, a total of 11 separate sections of rivers and tributaries were censused in varzea forest. Each section averaged 7 km in length and was censused up to 3 times. Censuses in the unhunted sites in varzea forest were conducted during the month of June 1996. Censuses in the hunted sites in varzea forest were conducted in the months of April through June 1995 and June through July of 1996. Censuses in the unhunted sites of upland forest were conducted during June 1997, and in the hunted sites during February, March, and April 1997.

Not all species were recorded during all of the censuses. I differentiated between interior forest dwelling species, (tinamous, cracids, trumpeters, wood-quails and doves), and species of open habitats (anhingas, herons cormorants, ducks, parrots, macaws, toucans). Species of open habitats are those that inhabit lakes, rivers and the top of the forest canopy. Interior forest species were recorded in all of the sites with the differing intensities of hunting. Species of open habitats were recorded in sites with heavy and moderate hunting and the control sites. Censuses were conducted by multiple parties. Each surveying party was composed of one biologist and a field assistant.

Population densities for all species except water birds were estimated using the program "Distance" (Laake et al. 1994). The program uses the probabilities of detection of randomly distributed objects (animals) to estimate density within the sampled area (Buckland et al. 1993, Pp. 2). To obtain the density of water birds, I used Overton's (1971) procedure. Because distances between the surveyor and the position of water birds were not obtained during water surveys, I used a fixed width (width of the watercourse surveyed).

$$D = N/W.L$$

Where D =Density (No individuals/km²), N =total number of individuals of a species observed, W = average width of watercourse surveyed, and L = total distance sampled. The approximate length of the water surveys was estimated by connecting points (geographical coordinates) taken along the water transects using a GPS device.

Catchment Area

The catchment area is the region where hunters range, and encompasses the kill sites for each species. Harvest within a catchment area provides a measure of hunting pressure per unit area (individuals harvested/km²). The location of kill sites was provided by hunters through the booklet-household method (Chapter 3). To locate the kill sites on a map, I converted time into distance. The time (provided by hunters) that hunters took to cover the distance between the village and a kill site, by foot or canoe, was converted into distance by 33 minutes/km. The time-distance conversion factor was determined from direct observations on the pace of hunters while searching for animals. Kill sites for each species was placed on a map of both hunting systems. The area (km²) encompassing the kill sites for each species was obtained using a computer program with cartographic capabilities (Idrisi 1997). To estimate the area encompassing the kill sites, the program assigns a value (km²) to each pixel and provides an estimate of the total area.

Hunting Pressure and Biological Parameters

Hunting pressure was obtained and described in Chapter 3. Biological parameters used in this study are described in Chapter 5, and are presented in (Table 4-2).

Table 4-2. Reproductive parameters, estimated r_{max} and λ_{max} and maximum harvest levels used in the evaluation of sustainability.

	Sexual maturity	Annual birth rate	Age of last reproduction	r_{max}^a	λ_{max}	Body mass (gr)	Proportion of production ^b
<i>Tinamus guttatus</i>	1.5	4.87	10	1.27	3.56	600	60
<i>Tinamus major</i>	1.5	4.87	10	1.27	3.56	1052	60
<i>Crypturellus undulatus</i>	1	3	10	1.4	4.06	540	60
<i>Crypturellus cinereus</i>	1	3	10	1.4	4.06	450	60
<i>Crypturellus variegatus</i>	1	3	10	1.4	4.06	384	60
<i>Crypturellus bartletti</i>	1	2	10	1.09	2.97	241	60
<i>Mitu tuberosa</i>	3	1.5	24	0.46	1.58	3060	20
<i>Penelope jacquacu</i>	3	2.25	20	0.55	1.73	1282	20
<i>Pipile cumanensis</i>	3	2.25	20	0.55	1.73	1425	20
<i>Ortalis guttata</i>	2.5	2.62	20	0.67	1.95	500	20
<i>Odontophorus stellatus</i>	1	1.87	14	1.05	2.86	310	60
<i>Cairina moschata</i>	2	8.62	12	1.25	3.49	2468	40
<i>Phalacrocorax olivaceus</i>	2	2.1	15	0.7	2.01	2010	40
<i>Ramphastos spp</i>	2	2.25	15	0.73	2.08	400	20
<i>Amazona spp</i>	2	2.25	20	0.73	2.08	486	20
<i>Ara spp</i>	2	1.5	20	0.6	1.82	1130	20
<i>Leptotila rufaxila</i>	1	1.5	12	1.25	3.49	157	60
<i>Psophia leucoptera</i>	3	1.2	15	0.42	1.52	990	20
<i>Angintha anhinga</i>	2	2.25	15	0.73	2.08	1235	40
<i>Ardea cocoi</i>	2	1.87	15	0.67	1.95	3200	40
<i>Cochlearius cochlearius</i>	2	1.87	15	0.67	1.95	656	40

^a r_{max} was obtained using Cole's (1954) equation.

^b Proportion of production obtained on the basis of species's longevity (see Robinson and Redford 1991).

Sustainability of Hunting.

Studies on wildlife utilization in Africa and the Neotropics have used two main approaches to evaluate the influence of harvesting on wildlife densities. The most common approach has been to compare densities in areas with differing hunting intensities (Peres 1990, Glanz 1991). Alternatively, the maximum potential sustainable harvest rate for each species can be estimated and compared with current harvest levels reported by hunters (Robinson and Redford 1991, Fitzgibbon et al 1995, Alvard et al 1996). Calculating sustainable harvest rates requires accurate data on population levels, population composition, and reproductive rates, which are rarely obtainable (Bodmer et al 1997). However, simple methods designed to provide estimates of sustainable harvest rates based on estimates of population densities, rates of population increase and sustainable yields, provide a first assessment of the impact of hunting on wildlife populations.

To evaluate the sustainability of bird hunting, I used 4 models. One approach (Stock-recruitment model) compares densities obtained in hunted and unhunted sites and examines whether current harvest is likely to be sustainable for a long term or it is likely to crash (Caughley 1977). The other three approaches (Harvest and Production models) assess the sustainability of hunting by comparing the rate of current harvest/km² with the rate of wildlife production/km². These models do not consider the density dependent effect of production, and assume that there is no immigration from other areas into the catchment areas.

Stock-recruitment model. The stock-recruitment model is an index of sustainability that relies on comparison of wildlife densities in hunted areas with densities

in unhunted or control areas. This model evaluates whether current harvest of Amazonian birds is using a safe management strategy or a risky management strategy. This model requires knowledge of population density in hunted areas (=pooled data obtained from sites areas with differing intensities of hunting) and unhunted areas. Population densities in unhunted areas are assumed to be in equilibrium and approximate the carrying capacity.

The stock-recruitment model is based on the logistic growth curve and predicts sustainable levels of harvest for different population sizes from time t to time $t+1$ (t =years); (McCullough 1987). Population sizes range from 0 (local extinction) to K (carrying capacity) (Figure 4-3). The 45° line on the graph represents no change in the population from t to $t+1$, whereas the parabola above the 45° line is the recruitment curve and represents the increase in population, also from t to $t+1$.

The distance between the 45° line and the recruitment line represents the increase of the population from one year to the next. A sustainable yield would be attained if the annual harvest takes the annual growth so that populations are maintained at the same base population on the initial point on the 45° line. A sustainable harvest could be conducted at any base population size, however, there is only one point that the sustained harvest is at maximum, or maximum sustainable yield (MSY) (Caughley 1977).

Harvesting population at the MSY is a risky strategy because a slight miscalculation that results in overharvesting the population could potentially lead to local extinction, if the same harvest is repeated year after year. Moreover, harvesting populations at small sizes (on the left of MSY) is also risky because a misjudgment in the harvest that is repeated year after year, will lead the population to local extinction even

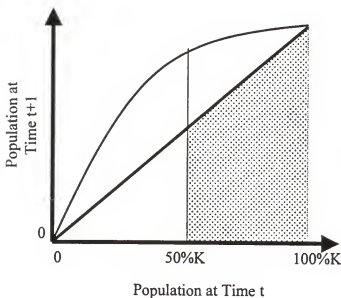
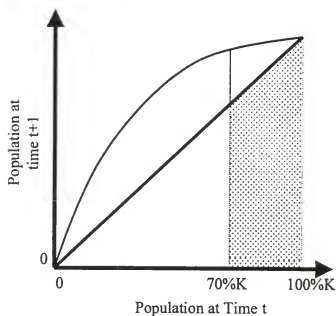


Figure 4-3. Representation of the stock-recruitment model for A) slow growing species, all species except for species of tinamous, and B) fast growing species, all tinamous. In both cases, the shaded area represents the range between MSY and carrying capacity. Harvest at population sizes within the shaded area represent a safe harvest strategy, whereas on the left of MSY, a risky harvest strategy.

faster (McCullough 1987). Conversely, harvesting species with large population levels (on the right of MSY) is a safe strategy because if misjudgments occur and the population is overharvested at the same rate year after year, the population will stabilize at the new population size and be sustainable for a long term. Thus, harvesting a species with a large base population is a safe management strategy since it is less likely to result in the extirpation of the population (McCullough 1987).

The rate of population change from time t to time $t+1$ depends on (N =population size) and (r =rate of population increase) ($dN/dt=rN(1-N/K)$) (Gotelli 1995). Species that show low rates of population increase have low values of r_{max} , then among these species, the rate of population change is more influenced by values of (N) than by rates of population increase. This relationship indicates that the maximum MSY among species with low rates of population increase (r_{max}) is realized at population sizes closer to the carrying capacity than species with high r_{max} .

MSY's have been estimated for rodents ($K/2$) (Caughley 1977), and ungulates (0.57-0.62% K) (McCullough 1982, Robinson and Redford 1991). Based on estimates of intrinsic rate of population increase (Chapter 5) and those proposed for species with broad similarities in reproductive productivity (Nichols and Haramis 1980), Amazonian birds were separated into fast and slow growing species. Among species in this study cracids, trumpeters, parrots, macaws, toucans and herons have low intrinsic rates of population increase (r_{max}), whereas species of the tinamous, wood-quails and doves have high values of r_{max} (Chapter 5). The stock-recruitment model assumes that for species with high rates of population increase, population densities in the hunted sites that are above $K/2$ represent a safe harvest strategy while for species with low rates of

population increase populations densities above $0.7\%K$ would represent a safe harvest strategy.

Production model. Production is defined as the addition to the population (through births and immigration), whether these animals leave (through death and emigration) or survive to the end of the specified time period (in this case one year). The production model evaluates whether an actual harvest is possibly sustainable under hypothetical conditions of maximum wildlife production (Robinson and Redford 1991). The model's principle is that hunters can take a proportion of P_{max} (maximum wildlife production), using $P_{max} = (0.6K * \lambda_{max}) - 0.6K$, where λ = finite rate of population increase, determined from the exponential of r_{max} (intrinsic rate of population increase). K is the density at carrying capacity. In this study, densities obtained from unhunted areas were assumed to approximate the carrying capacity. This model assumes that the maximum rate of production occurs at $0.6K$, that populations can be sustainably harvested so they remain at or near $0.6K$. Because the method of calculating the intrinsic rate of population increase (Cole 1954) assumes no pre-reproductive or adult mortality, Robinson and Redford (1991) suggested using the average life span of a species as an index of the number of animals that would have died in the absence of human hunting. Based upon species life span and rates of natural mortality, the model proposes that the proportion of the annual production that can go into harvest is 60% for very short-lived species (less than 5 years), 40% for short-lived species (between 5 and 10 years), and 20% for long-lived species (more than 10 years).

For comparison, I used an alternative method that estimates annual production based on the species' body mass and density (Banse and Mosher 1980). This model

differs from the previous one in the estimation of production only. The estimation of production rates uses the relationship of annual production/mean biomass by:

$$\text{Log}10(P/B) = a + (-b)\text{Log}10(M)$$

Where P includes both the addition of more animals and also increases in their average size. M is the mean Kcal equivalent of adult body mass, and B is the mean biomass obtained from the density at carrying capacity times M. The terms \underline{a} and \underline{b} scale the relationship between production and biomass. This study uses the coefficients $a = 1.11$ and $b=0.33$. These values are obtained from actual data sets that examine the relationship between annual production and biomass on vertebrates of varying sizes (Banse and Mosher 1980). This method of estimating production does not consider population size, composition of the population nor growth and mortality patterns.

Harvest model. The harvest model evaluates the impact of hunting by comparing hunting pressure with production (individuals/km²); both obtained from the catchment areas used by hunter (Bodmer 1994). Production is estimated by:

$$P = (0.5D) \times (0.75C \times N)$$

where P=Production (individuals/km²), and D= Density discounted by 50% because only female reproduce, and it is assumed that populations maintain a 1:1 sex ratio. The (C*N) term represents female productivity where: C=Species average clutch size discounted by 75% because this is the proportion of pairs among Neotropical birds that annually have one successful nest, a liberal estimate by Skutch (in Buckley et al. 1985), and N=Minimum number of nesting attempts obtained from published data and the span of a species breeding seasonality (Chapter 5).

The annual production is then divided by the annual hunting pressure. This yields the percentage of production taken by hunters. As in the previous models, the harvest model also assumes that the proportion of production that can be harvested sustainably is 60% for very short-lived species, 40% for short-lived species, and 20% for long-lived species.

Limitation of the Data Sets

There were several factors that must be considered when interpreting these results. One, the results on population abundance were based on a single unhunted area and a single area for each of the intensities of hunting. As a consequence natural variation in these sites may have a substantial impact on the relative abundance values and population density estimates for the avian taxa. In addition, in some cases this results were based on a small number of sightings over a short period of time at a single site that can also influence the relative abundance values and population density estimates. Two, some reproductive parameters were obtained from captive populations. While reproductive parameter from captive birds tend to over estimate values, because I attempt to model wild populations, when available, I used lower values reported in the literature. Three, distance to kill sites were estimated from data on time that hunters took to reach such kill site. However, time to reach the same kill site varied from hunter to hunter. I opted to obtain the average time when varying times were provided for the same distance. Four, the models used to evaluate sustainability use assumptions that are not necessarily met. The models are intended to provide a first estimate of the influence of hunting on Amazonian birds.

Results

Population Abundance in Unhunted Sites

I investigated species abundance (individuals/100 km) in unhunted sites (control) to examine whether populations differ in conditions of equilibrium (=without human hunting) and the implications of population size at equilibrium on population decline from hunting. The test of homogeneity indicates that species differed in abundance in the unhunted sites within upland ($\chi^2=29.3$, $df=18$, $P<0.000$), and within varzea forest ($\chi^2=34.4$, $df=18$, $P<0.000$). Abundance showed a good deal of variation ranging from 2-59 individual/100km in upland forest and 7-56 individual/100 km in varzea forest (Table 4-3). *P. leucoptera* and *P. jacquacu* have the greatest abundance in upland forest and relatively high abundance in varzea forest. Piscivorous birds were clearly more abundant in varzea forest. Other species varied in their abundance between forest types, suggesting that ecological differences between varzea and upland forest may be a determinant of population abundance. However, among species included in this study, data do not support the prediction of greater population abundance in varzea forest than in upland forest (Emmons 1984, Peres 1997) ($df=28$, $t=-0.5$, $P=0.3$).

Influence of Hunting on Bird Populations

I examined the association between hunting on Amazonian birds and changes in population abundance by measuring population abundances observed in sites subject to differing intensities of hunting and an unhunted or control site. Among interior forest species, the main effects indicate that the intensity of hunting influenced differences in population abundance ($P=0.00$) and this was consistent in the two forest types ($P=0.00$)

Table 4-3. Relative abundance, sampling effort, and number of individuals counted in the unhunted sites in upland and varzea forest. Censuses in upland forest were conducted during June 1997 and in varzea forest during June 1996.

Interior forest species	Relative abundance (individual/100 km)		Total number of individuals sighted in forest type		Number and total length of trails (km)				χ^2	P
	Upland	Varzea	Upland	Varzea	Upland		Varzea			
					Trail	Length	Trail	Length		
<i>Tinamus major</i>	10	18	43	71	7	30	8	34	6.16	0.013
<i>Mitu tuberosa</i>	3	10	12	39	7	30	8	34	9.53	0.002
<i>Penelope jacquacu</i>	34	18	139	74	7	30	8	34	9.17	0.002
<i>Pipiple cumanensis</i>	6	10	31	40	7	30	8	34	18.4	0.00
<i>Ortalis gutatta</i>	2	3	8	11	7	30	8	34	0.2	0.68
<i>Psophia leucoptera</i>	59	34	254	137	7	30	8	34	4.66	0.03
Species of open habitats										
<i>Cairina moschata</i>	4	9	5	7	4	21	4	18	1.04	0.31
<i>Phalacrocorax olivaceus</i>	3	27	4	21	4	21	4	18	16.7	0.00
<i>Ramphastos spp</i>	34	7	95	21	5	19	4	16	26.4	0.00
<i>Amazona spp</i>	18	8	49	22	5	19	4	16	3.67	0.05
<i>Ara spp</i>	18	9	72	24	5	19	4	16	2.81	0.09
<i>Anginha anhinga</i>	4	19	5	27	4	21	4	18	11.75	0.00
<i>Ardea cocoi</i>	20	56	26	78	4	21	4	18	13.5	0.00
<i>Cochlearius cochlearius</i>	3	24	4	33	4	21	4	18	16.7	0.00

^a Test of independence comparing birds counted on the total number of km censused in upland and varzea forest.

(Table 4-4). Changes in population abundance with the intensity of hunting were associated to species ($P=0.00$), and this was also consistent in both forest types ($P=0.00$). Forest type was not associated with changes in population abundance from hunting ($P=0.5$) and this was consistent among sites with the differing intensity of hunting ($P=0.09$).

Table 4-4. Summary statistics for the factorial ANOVA comparing population abundances (individuals/100km) of interior forest species in sites with differing intensities of hunting (=IH). Factors are; species, forest type, and intensity of hunting.

Source	df	Mean square	F	P
Species	7	16.7	18.8	0.000
Forest type	1	0.63	0.5	0.500
IH	7	8.9	7.4	0.000
Species*forest type	7	10.7	8.4	0.000
Species*IH	21	9	8.3	0.000
Forest type*IH	9	2.9	2.4	0.090

Among species of open habitats the intensity of hunting appeared not to be associated with changes in population abundance ($P=0.14$), and this was consistent among species and forest type ($p=0.5$) (Table 4-5). Species appeared to differ in abundance in function of forest types rather than variation in the intensity of hunting.

Table 4-5. Summary statistics for the factorial ANOVA comparing population abundances (individuals/100km) of species of open habitats in sites with differing intensities of hunting (=IH). Factors are; species, forest type, and intensity of hunting.

Source	df	Mean square	F	P
Species	7	17.7	16	0.000
Forest	1	21.3	19.2	0.000
IH	1	3.01	2.7	0.140
Species*Forest	7	19.7	13	0.000
Species*IH	7	7.1	1	0.500
Forest*IH	1	0.5	0.5	0.520

Population abundance in Sites with Differing Intensities of Hunting

Having shown that changes in population abundance appeared to be associated to the intensity of hunting, but the differences in population abundance varied among species and forest type, I examined species' variation in population size with the intensity of hunting. This analysis uses the Jonckheere-Terpstra test (Hollander and Wolfe 1999). This procedure tests the hypothesis $H_0 = \mu_1 = \mu_2 = \mu_3 = \mu_4$ versus $H_a = \mu_1 \leq \mu_2 \leq \mu_3 \leq \mu_4$. Some species declined in population abundance with the intensity of hunting while others did not (Table 4-6). In upland forest, the large cracids *M. tuberosa*, *P. cumanensis*, *P. jacquacu* and the trumpeter *P. leucoptera* declined with the intensity of hunting (Jonckheere-Terpstra = 4.67, $P = 0.004$). In contrast, tinamous and the small cracid *O. guttata* maintained similar abundances across the hunted and control sites (Jonckheere-Terpstra = 0.37, $P = 0.65$).

In varzea forest, the results were similar (Table 4-7). The large cracids and trumpeters declined with the intensity of hunting (Jonckheere-Terpstra = 3.77, $P = 0.009$). In contrast, species of the tinamous and the small cracids *O. guttata* did not show decline with the intensity of hunting (Jonckheere-Terpstra = 1.04, $P = 0.12$).

Among species of open habitats the intensity of hunting did not influence changes in population abundance. This was observed among species in upland forest (Table 4-8), and in varzea forest (Table 4-9).

Table 4-6. Relative abundance (individuals/100km) of interior forest species recorded at each of the sites with differing intensities of hunting in upland forest.

	Heavy			Moderate			Light			Control		
Species	R.a ^a	Trails	Length	R.a ^a	Trails	Length	R.a ^a	Trails	Length	R.a ^a	Trails	Length
<i>Tinamous guttatus</i>	8	4	15	8	14	56	5	3	12	3	7	30
<i>T. major</i>	6	4	15	10	14	56	14	3	12	10	7	30
<i>Crypturellus variegatus</i>	6	4	15	4	14	56	2	3	12	3	7	30
<i>C. Bartletti</i>	5	4	15	2	14	56	2	3	12	3	7	30
<i>Mitu tuberosa</i>	0	4	15	2	14	56	3	3	12	3	7	30
<i>Penelope jacquacu</i>	7	4	15	36	14	56	25	3	12	34	7	30
<i>Pipile cumanensis</i>	0	4	15	2	14	56	3	3	12	6	7	30
<i>Ortalis guttata</i>	8	4	15	1	14	56	0	3	12	2	7	30
<i>Psophia leucoptera</i>	0	4	15	29	14	56	43	3	12	59	7	30

^a Relative abundance (individuals/100 km)

Table 4-7. Relative abundance (individuals/100km) of species of open habitat recorded at sites with differing intensities of hunting in varzea forest.

	Heavy			Moderate			Light			Control		
Species	R.a ^a	Trails	Length	R.a ^a	Trails	Length	R.a ^a	Trails	Length	R.a ^a	Trails	Length
<i>Tinamus major</i>	8	4	16	19	5	20	12	7	28	18	8	34
<i>Crypturellus undulatus</i>	15	4	16	8	5	20	3	7	28	8	8	34
<i>C. cinereus</i>	10	4	16	5	5	20	4	7	28	3	8	34
<i>Mitu tuberosa</i>	0	4	16	0	5	20	2	7	28	10	8	34
<i>Penelope jacquacu</i>	0	4	16	0	5	20	7	7	28	18	8	34
<i>Pipile cumanensis</i>	5	4	16	0	5	20	11	7	28	10	8	34
<i>Ortalis guttata</i>	26	4	16	5	5	20	3	7	28	3	8	34
<i>Psophia leucoptera</i>	0	4	16	0	5	20	2	7	28	34	8	34

^a Relative abundance (individuals/100 km)

Table 4-8. Relative abundance (individuals/100 km) of species of open habitats recorded at the unhunted and the hunted sites in upland forest. The Chi-square test of independence shows differences in proportions between number of km surveyed and number of individuals sighted at each site.

Upland	Unhunted			Hunted				
Species	R.a ^a	Trail	Length	R.a ^a	Trail	Length	χ^2	P
<i>Cairina moschata</i>	4	4	21	2	5	28	0.72	0.12
<i>Phalacrocorax olivaceus</i>	3	4	21	0	5	28	1.52	0.22
<i>Ramphastos spp</i>	34	5	19	38	6	22	0.21	0.65
<i>Amazona spp</i>	18	5	19	27	6	22	1.10	0.30
<i>Ara spp</i>	18	5	19	27	6	22	1.20	0.27
<i>Anghinga anghinga</i>	4	4	21	3	5	28	0.00	0.97
<i>Ardea cocoi</i>	20	4	21	15	5	28	0.50	0.50
<i>Cochlearius cochlearius</i>	3	4	21	2	5	28	0.02	0.88

^aRelative abundance.

Table 4-9. Relative abundance (individuals/100 km) of species of open habitats recorded at the unhunted and the hunted sites in varzea forest. The Chi-square test of independence shows differences in proportions between number of km surveyed and number of individuals sighted at each site.

Varzea	Unhunted			Hunted				
Species	R.a ^a	Trail	Length	R.a ^a	Trail	Length	χ^2	P
<i>Cairina moschata</i>	9	4	18	2	5	31	1.30	0.25
<i>Phalacrocorax olivaceus</i>	27	4	18	9	5	31	4.70	0.03
<i>Ramphastos spp</i>	7	4	16	19	6	24	3.73	0.05
<i>Amazona spp</i>	8	4	16	6	6	24	0.41	0.53
<i>Ara spp</i>	9	4	16	5	6	24	0.83	0.36
<i>Anghinga anghinga</i>	19	4	18	19	5	31	0.01	0.91
<i>Ardea cocoi</i>	56	4	18	51	5	31	0.68	0.20
<i>Cochlearius cochlearius</i>	24	4	18	13	5	31	2.38	0.12

^aRelative abundance.

Evaluation of the Sustainability of Hunting

Catchment area. I examined the hunting pressure per unit area by comparing the harvest with the area where hunters ranged. Mean distances to kill sites differed among species in varzea forest ANOVA ($df=18$ $F=40.6$, $P=0.000$) and in upland forest ($df=19$, $F=37.6$, $P=0.000$). Longer distances to kill sites were associated with large birds and shorter distances with small birds in upland forest (Figure 4-4a) and in varzea forest (Figure 4-4b). In upland forest, large cracids *M. tuberosa*, *P. jacquacu*, *P. cumanensis* and the trumpeters *P. leucoptera* were hunted near the settlement as well as distant from it (Table 4-10). In varzea forest most large cracids and trumpeters appear to have been extirpated from within a radius of 6 km from the settlement. No bird was reported taken by hunters or sighted during censuses within this distance. The cracid *P. cumanensis* was rarely taken within 6 km of the village (9 individuals reported taken). The variation in distance to kill sites among large birds suggests that the impact of hunting is greater nearer the settlements than further. Kill sites of large and preferred (species that combine a good quality meat with large body size) species encompassed larger areas than those small or less preferred species (Table 4-10). In upland forest the catchment area used to procure large species was greater (by 352%) than the area used to procure small and less preferred species.

Likewise, in varzea forest, the area used to procure large and preferred species was greater (by 343%) than the area used to procure small and less preferred species.

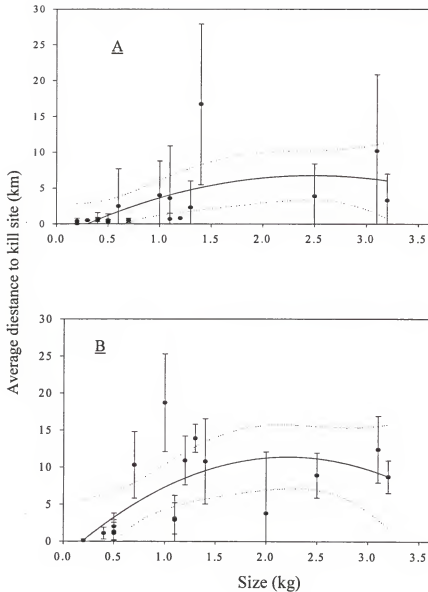


Figure 4-4. Relationship between bird size and distance of kill site. Circles (with stand error bars) represent the mean kill site distance from the village. The continuous line represents the best curve fitted and the dotted lines the 95% confidence interval of the regression in A upland forest ($R^2=0.6$, $P=0.001$), and B varzea forest ($R^2=0.51$, $P=0.01$).

Table 4-10. Average distances between the village to species kill sites. Kill sites were reported by hunters in the form of the time that it would take hunters to reach the kill site of each individual bird from the village. Time was converted into distance using a conversion factor (see text). Catchment area uses the area (km²) encompassing the kill sites for each species.

Species	Upland				Catchment Area (Km ²)	Varzea				Catchment area (Km ²)
	Mean time (hours)	Average distance to kill site (Km)	Range (Km)	n ^a		Mean time (Hours)	Mean distance (Km)	Range (Km)	n ^a	
<i>Tinamus guttatus</i>	1.25	2.5 ± 5.2	0.06 – 14	17	120					
<i>Tinamus major</i>	1.79	3.6 ± 7.3	0.03 - 24	33	120	1.47	2.9 ± 3.3	0.5 - 12	88	57
<i>C. cyrturellus cinereus</i>						0.61	1.22 ± 1.3	0.16 - 6	19	57
<i>Crypturellus undulatus</i>						0.7	1.3 ± 1.6	0.16 - 8	75	57
<i>Crypturellus variegatus</i>	0.3	0.6 ± 0.3	0.2 - 1	4	79					
<i>Crypturellus bartletti</i>	0.2	0.4 ± 0.4	0.1 - 1	4	79					
<i>Mitu tuberosa</i>	5.09	10.2 ± 10.6	0.12 - 24	17	460	6.5	12.4 ± 4.5	6 - 28	43	276
<i>Penelope jacquacu</i>	1.24	2.3 ± 3.7	0 - 24	95	460	6.6	13.9 ± 1.9	8 - 26	31	276
<i>Pipile pipile</i>	8.35	16.7 ± 11.2	0.1 - 24	16	460	5.4	10.8 ± 5.8	1 - 18	86	276
<i>Ortalis guttata</i>	0.25	0.5 ± 0.9	0.03 - 3	17	79	0.6	1.1 ± 1.02	0.16 - 3	23	57
<i>Cairina moschata</i>	1.95	3.9 ± 4.5	0.03 - 24	4	79	4.4	8.9 ± 3.03	4 - 14	19	57
<i>Phalaropus olivaceus</i>						1.9	3.8 ± 8.3	1 - 7	17	
<i>Ramphastos spp</i>	0.35	0.7 ± 0.87	0.02 - 3	25	79	0.6	1.1 ± 0.8	0.2 - 3	15	57
<i>Amazona spp</i>	0.13	0.3 ± 0.31	0.03 - 1	22	79	1	2 ± 1.8	0.7 - 8	28	57
<i>Ara spp</i>	0.3	0.7 ± 0.8	0.03 - 2	16	79	1.54	3.1 ± 2.1	1 - 8	21	57
<i>Leptotila rufaxilla</i>	0.01	0.02 ± 0.05	0 - 0.2	12	16	0.1	0.1 ± 0.2	0 - 1	23	6
<i>Psophia leucopetra</i>	1.9	4 ± 4.8	1 - 24	61	360	9.4	18.7 ± 6.6	10 - 32	10	276
<i>Anhinga anhinga</i>	0.42	0.8 ± 0	0.4	2	79	5.4	10.9 ± 3.3	3 - 16	23	57
<i>Ardea cocoi</i>	1.64	3.3 ± 3.7	0.06 - 12	20	79	4.4	8.7 ± 2.2	7 - 14	12	57
<i>Cochlerius cochlerius</i>	0.25	0.5 ± 0.3	0.3 - 0.9	3	79	5.16	10.3 ± 4.5	3 - 18	23	57

^aNumber of birds used to obtain average distance to kill site.

Species were procured from larger catchment areas in upland forest than in varzea forest (Wilcoxon signed ranks test $Z = -3.4$, $P = 0.001$).

Stock-recruitment model. The stock-recruitment model was used to evaluate the bird harvest in upland forest and varzea forest to see if the current harvests were being conducted in a safe or risky manner. In the hunted area of upland forest, densities of all four species of cracids, *C. moschata*, *Ara spp.* and the trumpeter *P. leucoptera*, were below their predicted MSY and on the risky side of the stock-recruitment model. In contrast, densities of all other species were above their predicted MSY and were being harvested on the safe side of the stock-recruitment model (Table 4-11, 12).

In varzea forest, the stock-recruitment model indicated that the base population size of *P. jacquacu*, *C. moschata*, *P. olivaceous*, and *Ara spp.* were below the predicted MSY. *P. leucoptera* was being harvested to a population level far below the species MSY, therefore, at a population size likely to become locally extinct (Table 4-11). *O. stellatus* also was below the predicted MSY, but given that hunters did not take the species, low abundance in the hunted grounds may be due to natural geographic variation in population abundance. The stock-recruitment model suggests that seven species in upland and six in varzea forest are being harvested to population levels below their predicted MSY. Moreover, *P. jacquacu*, *C. moschata*, *Ara spp.* and *P. leucoptera*, were being harvested to population levels below their MSY in both forest types. Therefore, the model suggests that the harvest of these species is using a risky strategy because harvest might be reducing the population size year after year, which is likely to result in local

Table 4-11. Results of the models used to evaluate the sustainability of current hunting in upland forest. Density of hunted populations used pooled data from all sites with differing intensities of hunting.

Species	Harvest Model		Production Model (Population growth)		Production Model (Biomass)		Stock-Recruitment Model	Harvest
	Density* Unhunted (No/km ²)	Density* Hunted (No/km ²)	Catchment area (km ²)	Proportion of production harvested (%)	Production (No/km ²)	Maximum sustainable harvest (No./catchment area)	Percentage of density at K in hunted area	
<i>Tinamus guttatus</i>	3.22	6.5	120	2.1	4.9	356	202	28
<i>Tinamus major</i>	9.68	8.1	120	6.5	14.9	1071	84	110
<i>Crypturellus variegatus</i>	4.89	3.4	79	2.2	9.0	425	70	9
<i>Crypturellus bartletti</i>	3.85	2.5	79	4.6	4.6	216	65	9
<i>Mitu tuberosa</i>	1.37	0.6	460	10.1	0.5	44	44	21
<i>Penelope jacquacu</i>	12.2	6.91	460	6.2	5.4	494	57	177
<i>Pipile cumanensis</i>	3.24	0.4	460	0.4	1.4	131	12	31
<i>Ortalis guttata</i>	0.61	0.27	79	112.5	0.3	6	44	24
<i>Odontophorus stellatus</i>	7.2	7.6	79	0.5	8.0	380	106	3
<i>Cairina moschata</i>	0.96	0.5	79	1.4	4.5	45	52	5
<i>Phalaacrocorax olivaceus</i>	0.4	0	79	0.0	0.2	8	0	0
<i>Ramphastos spp</i>	14.53	13.1	79	9.8	9.4	148	90	33
<i>Anas spp</i>	6.4	5	79	5.0	4.1	65	78	27
<i>Ara spp</i>	14	5.13	79	3.8	6.9	109	37	27
<i>Propheta leucophaea</i>	17.66	9.45	360	5.7	5.5	398	54	81
<i>Anhinga anhinga</i>	0.77	1.5	79	1.5	0.5	16	195	2
<i>Ardea cocoi</i>	3.65	5.5	79	5.1	2.1	66	151	24
<i>Cochlearius cochlearius</i>	0.6	1	79	0.9	0.3	11	167	3

*Density data using the DISTANCE program (Buckland et al 1993) is provided on Appendix D.

Table 4-12. Results of the models used to evaluate the sustainability of current hunting in varzea forest. Density of hunted populations use pooled data from all sites with differing intensities of hunting.

Species	Harvest Model			Production Model (Population growth)		Production Model (Biomass)		Stock Recruitment Model	Harvest
	Density* Unhunted (No/km²)	Density* Hunted (No/km²)	Catchment area (km²)	Production (No/km²)	Proportion of production harvested (%)	Production (Ind./km²)	Maximum sustainable harvest (Ind/catchment area)		
<i>Tinamus major</i>	10.7	7.3	57	12.8	16.3	16.4	556.3	68.4	118
<i>Crypturellus undulatus</i>	6.3	5	57	7.5	34.0	11.6	393.4	79.0	144
<i>Crypturellus cinereus</i>	4.9	8.5	57	8.5	7.1	9.1	307.0	172.1	34
<i>Mitu tuberosa</i>	2.4	2.2	276	1.7	15.6	0.8	45.8	92.8	71
<i>Penelope jacquacu</i>	5.7	3.15	276	2.8	6.6	2.5	137.7	55.6	52
<i>Pipile cumanensis</i>	6.4	10.7	57	9.6	4.7	2.8	156	166	125
<i>Ortalis guttata</i>	0.5	3.2	57	3.2	17.1	0.3	3.3	627.5	31
<i>Odontophorus stellatus</i>	14.0	4.6	57	4.3	0.8	15.6	530.5	32.8	1
<i>Cairina moschata</i>	2.5	0.55	57	1.5	25.2	3.8	85.8	21.7	22
<i>Phalacrocorax olivaceus</i>	7.3	3.3	57	2.5	2.9	4.4	99.8	45.5	4
<i>Ramphastos spp</i>	5.1	7.4	57	5.6	8.0	3.3	37.2	145.1	25
<i>Amazona spp</i>	7.1	6.3	57	6.3	8.7	4.6	51.8	88.7	31
<i>Ara spp</i>	7.7	3.4	57	2.6	25.7	3.8	43.0	44.1	37
<i>Leptotila rufaxilla</i>	15.5	18.8	57	15.0	4.6	23.0	780.1	121.5	39
<i>Psophia leucoptera</i>	13.2	0.6	276	0.4	13.1	4.1	227.7	5	13
<i>Anhinga anhinga</i>	5.7	8.24	57	8.2	8.4	3.7	83.2	144.3	39
<i>Ardea cocoi</i>	15.0	18.7	57	17.5	2.1	8.6	194.1	124.7	21
<i>Cochlearius cochlearius</i>	6.7	5.5	57	5.1	23.4	3.8	86.7	82.1	68

*Density data using the DISTANCE program (Buckland et al 1993) is provided on Appendix E.

extinction if steps are not taken to increase the base population to level above 0.7K (Caughley 1977).

Production model. The production model was used to evaluate the harvest of Amazonian birds in upland and varzea forest to see if current harvest is possibly sustainable under conditions of maximum population production (Robinson and Redford 1991). The production models compare harvest (individuals/km²) with maximum production (individuals/km²). The production model using population growth (Robinson and Redford 1991) and biomass (Banse and Mosher 1980) to estimate maximum production indicated that the harvest of birds is being conducted mostly within the limits of maximum production levels in upland forest (Table 4-11) and in varzea forest (Table 4-12). In varzea forest the model suggested that *M. tuberosa* is being hunted above the maximum limits of production; therefore, the model indicated that this species is being overhunted. The other species are being harvested within the limits of maximum production levels. While the production model indicated that most species are being harvested below the limits of maximum production estimated by the model, it can not be inferred that current harvest is sustainable (Robinson and Redford 1991).

Harvest model. The harvest model was used to determine if current harvest from a catchment area (individuals/km²) exceeds production (individuals/km²). The harvest model suggested that most species compensated for harvest, and appeared sustainable at the current level of harvest in upland forest and varzea forest (Tables 4-11, 12). Only *Ara spp.* in varzea forest appeared not to be compensating for current harvest, which was taking a higher (26%) proportion than the 20% sustainable.

Discussion

Sustainable use of wildlife is an innovative approach to biodiversity conservation (Freese 1997). This approach embraces the notion that sustainable harvest of wildlife could help prevent forest transformation by adding value to standing forest (Balmford and Turyaho 1992). Harvesting of wildlife is one of the few benefits available to local communities that offset some of the direct and indirect costs of forest conservation (Bodmer et al 1994). However, if sustainable harvest is likely to help forest conservation, it is necessary to know how harvest influences population abundance of species in differing environments.

Upland and varzea forest ecosystems do not support birds at the same level of abundance. Piscivorous species were more abundant in varzea forest, perhaps because aquatic habitats and fish are more abundant than in upland forest (Bayley et al. 1994), and abundance of resources often correlates with greater abundance of animals (Emmons 1984, Loiselle and Blake 1991). This rationale is not clear among frugivorous birds. Rich soils and greater fruit availability in varzea forest (Chapter 2) would be expected to result in greater abundance of frugivorous birds (Emmons 1984, Janzen 1974, Peres 1996b). However, frugivorous species did not show a concomitant greater abundance in varzea forest.

Differences in flood regimes between upland and varzea forest appeared not to influence population abundance. Flood periods of 2-4 months in duration would be expected to influence populations of at least the most terrestrial foragers (all of the tinamous, wood-quails, and trumpeters) and semi-arboreal species (*M. tuberosa* P. *jacquacu*, and *P. cumanensis*). However, most ground foragers showed either similar or

greater abundance in the flood-prone varzea than in upland forest. All ground foragers are sedentary species that maintain year round territories (except perhaps for *P. cumanensis*) (Franco and SantaMaria 1997, Delacour and Amadon 1973, Forti and Vispo, In Press). Thus, it appears that species maintain similar abundances regardless of differences in flood regimes.

Variation in abundance in unhunted sites also may be influenced by ecological factors other than differences in food availability and flood regimes. Abundances reported in this study were relatively lower than those reported from unhunted sites throughout the species distribution, perhaps due to the larger scale sampling of this study relative to most studies on Table (4-13). Furthermore, the abundances of Amazonian birds is known to vary sometimes in seemingly continuous forest (Hilty 1994). Hence, the need to gather data on abundance from a site in order to evaluate sustainability at the local level.

Mean kill site and Catchment area. Mean kill site distance differed among species and was positively correlated with body size. Greater distance to kill sites is an indicator of wildlife depletion and covariates with the age of the settlement (Vickers 1980). This was observed in the two villages studied. In the younger settlement in upland forest, a greater number of species (52%) were procured within 1.5 km from the settlement, whereas in the older settlement in varzea forest, only 29% were procured within 1.5 km from the settlement.

Species catchment areas were smaller in varzea than in upland forest. A larger human population density and greater wildlife depletion near the settlement in varzea forest would suggest that hunters had to spread their search over wider areas to procure

Table 4-13. Population density (No. Individuals/km²) obtained in unhunted sites throughout the species geographic distribution, where F-P=Floodplain forest and U-F=Upland forest. The method to estimate density varied across studies.

Species	Forest type							
	F-P ¹	Gallery & F-P ²	U-F ³	F-P ⁴	F-P ⁵	F-P ⁶	U-F ⁷	F-P ⁸
<i>Tinamus major</i>	25.8				4.1 7.9	18.0	9.7	10.7
<i>Crypturellus spp</i>	25.8				21 8.3	18.0	4.4	5.6
<i>Mitu tuberosa</i>	5.3			16.0	5.6 25	5.0	1.4	2.4
<i>Pipile cumanensis</i>	4.5				3.7 8.3	5.0	3.2	6.4
<i>Penelope jacquacu</i>	2.9	19.9 - 22.4	8.0 - 28.0		3.1 6.2	2.0	12.2	5.7
<i>Ortalis guttata</i>	2.17		0.0 - 14.0		26 11.8		0.6	0.5
<i>Psophia leucoptera</i>	2.0					9.0	17.7	13.2

1) Gonzales 1998. Varzea forest subject to 2-5 month floods, DISTANCE (Buckland et al 1993).

2) Silva and Strahl 1991. Forest type not specified, Variable distances (Overton 1971).

3) Wallace et al In press. Forest not subject to riverine floods, DISTANCE (Buckland et al 1993).

4) Gutierrez 1997. Forest subject to seasonal 1-5 day riverine floods, Variable distances (Overton 1971).

5) Mitchel and Raez-Luna 1991. Forest subject to seasonal 1-5 day riverine floods, Effective distance (Whitesides et al 1988).

6) Terborgh et al 1987. Forest subject to seasonal 1-5 day riverine floods, Various methods.

7) This study. Forest not subject to riverine floods, DISTANCE (Buckland et al. 1993).

8) This study. Forest subject to 1- 4 months riverine floods, DISTANCE (Buckland et al. 1993).

wildlife. However, catchment areas in the more densely populated varzea forest were smaller than in the less densely populated upland forest. Population density appeared not to determine the size of the catchment area. This is farther supported by the lack of association between human population density with the size of their corresponding catchment areas obtained from published data on 11 hunting studies in the Neotropics (Spearman rho = 0.3, P = 0.8). This suggests that factors other than human population density influences the size of catchment areas.

Vegetation type, importance of fishing, and agriculture for a human settlement have been suggested to influence the size of the catchment area used by hunters (Hill and Hawkes 1983, Stearman 1990, Yost and Kelley 1983, Ayres and Ayres 1979). In varzea forest, the hunting grounds were limited by forest of difficult access. In addition, fishing and agriculture were more important than in upland forest (FPCN 1994), which may signify less pressure to procure terrestrial wildlife and to expand the area of their hunting grounds. Exploratory surveys in the grounds adjacent to catchment areas used by hunters in varzea forest revealed contrasting greater abundance of wildlife, which was apparently not utilized by hunters. In contrast, in upland forest there is less potential for agriculture and less availability of fish (Brack 1990) which result on a greater pressure over land animals. In addition, upland forest is, overall, easier to access (personal observation). Variation in the need for animal protein from terrestrial wildlife, and variation in the accessibility to the forest help explain differences in size of catchment areas between upland and varzea forest.

Low hunting pressure in large areas is more likely to allow wildlife to compensate for harvest (McCullough 1996). Households in upland forest dispersed along a 24-km stretch of a meandering a river (Chapter 3), and used mostly non-overlapping hunting grounds at the rate of 1 consumer/5.4 km². Households in varzea forest concentrated along 3 km of riverbank, and hunting grounds were used by all village residents at the approximate rate of 1 consumer/2 km².

The hunted and unhunted sites in varzea forest may have been subject to differing ecological pressures. The hunted sites in varzea forest were located on an active floodplain, whereas the control or unhunted sites were located farther from the active

floodplain, and perhaps less exposed to the ecological constraints of severe floods. Due to its location, the hunted site may experience more intense riverine floods (Kalliola and Puhakka 1993) that may have contributed to naturally lower population abundance of the ground users *M. tuberosa*, *P. jacquacu*, *P. leucoptera* and their proneness to local extirpation from hunting. Evidence for this possible influence of site differences derives from changes in abundance showed by the wood-quail *O. stellatus*. This species showed a lower abundance in the heavily hunted area (active floodplain) in spite of not being taken by hunters.

Birds of open habitats did show differences in abundance between un hunted and hunted sites. In contrast to the mostly territorial interior forest birds, birds of open habitats were strong flyers that typically used wide areas in search for ephemeral sources of food (e.g., fruit and fish) (Snow 1981, Levey and Stiles 1992, Munn 1994). Birds from other areas may be moving into the catchment areas sampled making detection of the influence of hunting difficult (Novaro 1995, Peres 1996a). To conclude that hunting does reduce populations of birds of open habitats, additional evidence such as the rate of movements into the hunted area is required. In addition, this hypothesis would need to be thoroughly tested by long term studies on population variation at the regional level.

Sustainability of hunting. The models used to evaluate sustainability of harvest help provide an understanding of the impact of hunting on bird populations. The production models are useful for determining if current harvest is being conducted within the limits of maximum production levels. The harvest model is useful for evaluating the sustainability of hunting in an area, because it uses information on production and harvest from the field sites. The stock-recruitment model can be used to decide whether bird

harvest would be sustainable over longer periods, or if they would be vulnerable to population crashes. Numeric values represent general trends, and are interpreted in terms of results from all models and other results from this study.

The stock-recruitment model indicated that the harvest of 7 species (39%) in upland forest and 6 species (28%) in varzea forest was conducted to population levels that were below the estimated MSY and represents a risky harvest strategy. A weakness of this model is that it assumes that differences in density are caused by hunting (Robinson and Redford 1994). In this study increasing intensities of hunting were associated with decreasing populations abundances of the cracids *M. tuberosa*, *P. jacquacu*, *P. cumanensis* and the trumpeter *P. leucoptera*. Therefore, the stock-recruitment model indicated that hunting has reduced abundances of these species to current levels and may be leading them to local extinction. Harvest should be lowered so that populations can recover to levels above the predicted MSY. The model also suggests that *O. guttata*, *Ara spp.*, *C. moschata* are being harvested at population densities below the MSY. However, data did show an association between hunting intensity and differences in population abundance between the hunted and unhunted populations. The stock-recruitment model suggested that hunting of these species should be lowered so that populations can increase above the estimated MSY.

Predictions of the harvest model should be interpreted in relation to results from the stock-recruitment model. Because the harvest model compares production and harvest from hunted sites, it does not consider whether populations used to predict sustainability are harvested at base population sizes regarded as a safe harvest strategy - above MSY- or in a risky manner -below MSY-. It only predicts whether current hunting

is sustainable from a standing base population size. Therefore, the harvest model may still predicted sustainability in populations that are prone to crash. The harvest model predicts that *P. cumanensis* in upland and *Ara spp.* in varzea forest are being overhunted and this result concurs with those predicted by the stock-recruitment model.

With the exception of *M. tuberosa* in varzea forest, the two models using population growth and biomass to estimate production predicted that birds are being harvested within the limits of the species' maximum production. Moreover, the models suggest that most species could be harvested at greater than current, given the margin between current harvest and maximum production (Fitzgibbon et al. 1996). The production model predicts with a wide margin that most bird populations are harvested within the limits of maximum production. However, the model does not predict whether current harvest is sustainable (Robinson and Redford 1991).

Implicit in the calculation of the production and harvest models is the assumption that animals do not enter the catchment area. However, animal immigration from unhunted areas acts as a source that replenishes hunted areas (Novaro 1995, McCullough 1996). This may explain why birds of open areas, (non-territorial strong flier), appear not to be influenced by hunting. For example the arboreal and mobile frugivorous, *P. cumanensis*, although very rare, has not become locally extinct in the heavily hunted site of varzea forest as have other territorial and sedentary cracids and trumpeters.

The interpretation of predictions yielded by the models should be taken as an indicator of trends resulting from the observations in the two study sites and not as static constants. The purpose of the models is to provide a first assessment of the impact of

hunting on bird populations hunted by ribereño people. Moreover, models used here are subject to several assumptions that may not necessarily be met in conditions of this study.

In conclusion, my data support the hypothesis that hunting appears to be associated with differences in population abundance of some species while populations of others species appear to be influenced by hunting. Among species whose population sizes declined with the intensity of hunting (cracids and trumpeters), populations in varzea forest appeared to experience greater variation in population abundance in the hunted site relative to the unhunted sites. Trumpeters and guans showed significant decline in spite of being abundant in the unhunted site (Robinson and Wilcove 1989). Differences in the proportion of number of hunters per unit area, age of the human settlement, and settlement patterns appear to be associated with differences in the impact of hunting. *P. leucoptera*, *P. jacquacu*, *P. cumanensis*, *M. tuberosa* and *Ara spp.* are being hunted to population densities below the estimated MSY, therefore, current harvest may be leading them to local extinctions. Harvesting of these species should be lowered so populations can increase to levels above the predicted MSY in order to harvest these populations to populations sizes that represent a safe harvest strategy.

CHAPTER 5 ECOLOGICAL CORRELATES OF POPULATION DECLINE

Introduction

While some species show population decline associated with hunting, others maintain stable populations (Balmford 1996, this study). Species that are vulnerable to hunting typically have populations that are small, slow growing, and fluctuating (Terborgh and Winter 1980, Reid and Miller 1989). Other ecological traits associated with differential population declines are: large body size, high trophic position, poor dispersal/colonization ability, restricted geographical range, colonial and migratory habits, specialization on food or habitat resources, naïve attitudes towards novel predators, and lack of adaptation to high rates of predation (Reid and Miller 1989, Peltonen and Hanski 1991, Sieving 1992, Angermeier 1994, Reichel and Lemke 1994). Most of these traits reflect both sensitivity to decreasing habitat area and increasing isolation, and they have been observed in island studies (Terborgh and Winter 1989, Karr 1990). However, the reasons that some species of Amazonian birds subjected to hunting remain stable while others decline and become locally extinct are poorly understood.

Amazonian bird populations provide an opportunity to investigate correlates of population decline from hunting by humans. Amazonian birds differed in abundance (Chapter 4) and abundance could be an indicator of ecological suitability of the population to the habitat (Begon et al. 1990) and the potential of the population for harvest (but see Eisenberg et al. 1979). Ribereño hunters prefer species that are large and

have good quality (This study). Therefore, hunters are more willing to pursue certain species than others. But in order to harvest a bird, hunters first must detect it, decide whether to proceed to attempt a kill, and to make the actual kill. While preferred species are more likely to be pursued (Hames 1980, Hawkes et al 1997), species vary in the extent that they are detected (Fitzgibbon et al 1996), and in the ease that they can be killed. This is because; some species are more detectable by hunters than others; use habitats that are typically frequented by hunters; forage at different heights in the forest, and perform antipredator behaviors that differ in efficiency. These factors influence how often individuals of a species are taken (=hunting pressure), and greater hunting pressure often leads to population decline (Caughley and Gunn 1996). However, hunting pressure is does not always lead to population decline because species differ in their reproductive biology, and the capacity to compensate for individuals removed from the population (Caughley 1977).

In this study I analyzed ecological traits of Amazonian birds in an attempt to identify proximate causes of population decline from hunting. I first test the hypothesis that antipredator behavior differs among species. Then, I examined species body size, group size, position within the vertical height of the forest (PVF) where the individuals of a species is usually found, and population abundance at equilibrium (abundance in unhunted sites), in terms of the ratio of change in population abundance between unhunted and hunted sites to test the hypothesis that population decline from hunting does not occur randomly but it is prevalent among species with specific ecological characteristics. Subsequently, I examined species' breeding biology in terms of patterns

of population decline to test the hypothesis that the intrinsic rate of population growth is associated with the response of bird populations to hunting.

Methods

Study Site

This study took place in sites in varzea and upland forest in northeastern Peru, state of Loreto, during May 1996 and February 1998 (sites are described in Chapter 4). Sites in upland and varzea forest were located in continuous forest not separated by any major barrier (e.g., Amazonian river) and had similar floristic composition within forest type (Encarnacion 1993).

Data on antipredator behavior, group size, position within the vertical length of the forest, and group size, were obtained from wild birds in surveys along line transects (described in Chapter 4). Data on breeding biology were obtained from wild birds, published literature on captive populations, and birds kept as pets by village residents. A common practice among rural Amazonians is collecting young wild birds to be hand-raised. Data on brood size, and annual breeding seasonality, was obtained from interviews with hunters on dates of collection and clutch sizes of nests where their pet birds were collected. Data on pet birds were gathered at the following villages in upland forest: San Pedro (W73°11'59", S4°20'14.3"), Carolina (W4°25'10.8", S71° 47'40.6"), San Felipe (W71°57'35", S4°18'06"), Esperanza (W71°58'29" S4°14'03), Buen Jardin (W72°08'53", S4°22'00"), and Pavaico (W72°27'33", S4°34'89"). Likewise, data on pet birds were obtained from the following villages in varzea forest: Nueva Esperanza (W75° 05'47.9", S4° 48'47.8"), Maipuco and San Antonio (W75°07'01", S4°49'17.7"), and San

Pedro-Rio Mara on (W75 11'09",S4 39'16.1"). Data on relative abundance, and hunting pressure were obtained by methods described in Chapters 3 and 4.

Change in population Abundance

I examined the association between hunting and species' change in population abundance by obtaining the ratio of change between un hunted and hunted populations. This comparison assumes that abundances were equal prior to hunting. Population abundance in the hunted sites (3 populations in upland and 3 in varzea forest) uses the pooled data from all sites with differing intensities of hunting used in chapter 4.

Habitat Use

From exploratory observations and comments from hunters it became evident that *M. tuberosa* and *P. cumanensis* were associated to forest edges that border bodies of water. Because bodies of water (e.g., rivers and lakes) are frequented by river o people for fluvial transportation and fishing, I examined the association between these species' habitat use with hunting pressure. I do this by comparing the frequency of encounters with these species at a) borders of bodies of water, and b) away from bodies of water (no body of water visible from the point where the bird was observed. Then, I compared the kill site reported by hunters to examine the frequency that these birds were shot by hunters in habitats bordering bodies of water.

Position Within the Vertical Height of the Forest (PVF), Group Size, Body Size, and Abundance in Unhunted areas.

Group size and (PVF) for each species used pooled data on these traits obtained in upland and varzea forest. A comparative analysis indicated that (PVF) ($df=34$, $t=0.01$, $P=0.9$), and group size ($df=34$, $t=0.02$, $P=0.9$) did not differ between species in upland and varzea forest. (PVF) was defined as the average distance from the ground to each bird's initial position along the vertical length of the forest. Vertical distances were visually estimated for each species. Visual estimations were rehearsed with mock trials to accuracy within ± 5 meters.

Body size. Body mass was obtained from published literature (Delacour and Amadon 1973, Dunning 1992). Measurements from birds shot by hunters were inaccurate and difficult to obtain. Hunters often consumed birds during hunting trips, and carcasses brought to the village were often missing body parts as part of the preparation process before cooking (Chapter 3).

Group size. I recorded the group size of birds sighted along the line transects used in Chapter (4). A group was defined as individuals of the same species found in proximity to one another. Individuals of the same species congregated in sources of food were regarded as a group (e.g., fruiting tree).

Anti-Predator Behavior

Antipredator behavior was defined as actions performed by a prey that reduces the probability that it is captured by a predator (Abrams 1990). Studies on antipredator behavior have used recordings of stress calls or dummy predators to quantify this behavior (Abrams 1990). I assumed that actions performed by birds in response to my

presence were the same as those they would perform in the presence of a hunter. The distance of escape (=DE) was regarded as a measure of efficiency of a species antipredator behavior. A species average DE measures the length between a bird's initial position and its location 10 seconds later.

I measured each species' average DE, a measure of flushing distance, assuming that longer distances reduced the chances of obtaining a clear shot, or further pursuit of the prey by a hunter, than shorter distances. I estimated the distance between a bird's initial position and its location 10 seconds later. I counted 10 seconds from the time that the bird became aware of the presence of a hunter, as indicated by a change from normal behavior (e.g., feeding, preening, or relaxed posture) to a characteristic alert behavior (e.g., behavior characterized by stretched neck, emission of alarm calls and constant vigilance of the potential predator). DE ranged from 0 to a maximum of 25 meters from the surveying trail because visibility at farther distances became difficult and 15-20 meters is the approximate range that hunters can get a clear shot in conditions of lowland humid forest (Smith 1976). For birds found in groups, I obtained the DE of a randomly selected bird. A bird that was assigned 0 m indicates that it did not move in 10 seconds after becoming aware of the hunter's presence, while 25 m indicates that it flew at least 25 m within a 10 second period. Because the distance between the hunter and the initial position of a bird may influence the DE (Ducey and Brodie 1991), I consider only birds whose initial position was within 10 meter from the surveying trail. DE was estimated visually. Visual estimation was previously rehearsed in selected sites.

Antipredator behaviors were classified as active and passive strategies. In a typical active strategy, a bird became out of sight upon or within a few seconds after

reacting to the presence of a hunter. In a typical passive strategy, birds remained within sight (moving from its initial position or not) for up to 10 seconds after becoming aware of the hunter's presence.

I differentiated between interior forest dwelling species, (tinamous, cracids, trumpeters, wood-quails and doves), and species of open habitats (anhingas, herons cormorants, ducks, parrots, macaws, toucans). Species of open habitats were those that inhabit lakes, rivers and the top of the forest canopy (Levey and Stiles 1992). This differentiation was made to account for the influence of structure of the forest among interior forest dwelling species versus no structure among open habitats dwelling species.

Data on antipredator behavior were obtained from unhunted sites and sites within hunted areas subject to light hunting pressure. These sites were sampled to avoid bias from behavior that may have been influenced by interaction with hunters (Ducey and Brodie 1991), and also because some species were missing or rare in areas heavily hunted.

Probability of Detection

To estimate the probability that a hunter detected a bird at increasing distances from a trail, I tape-measured the perpendicular distance between the trail and a bird's initial position upon sighting. Measurements were used to obtain the frequency distribution and the probability of detection curve at increasing distances from the trail. For birds observed on trees, the distance was taken from the trail to the point on the ground below the bird's position. For birds observed in groups, the initial position was

the point that represented the center of the group. Birds observed in groups were considered as a single entry (see Buckland et al 1993).

Morphology and Antipredator Behavior

Flight is an important part of the antipredator behavior. I examined species wing and tail morphology and related these measurements to species DE. I obtained the wing and tail areas and their aspect ratio, a measure of aerodynamic shape for an individual of each species. Wing and tail measurement were taken from tracings made on paper with the anterior edge of the wing held as extended as possible, and the tail closed and flattened, respectively (Fitzpatrick 1985). Tracings were obtained from live birds kept in households or birds shot by hunters. The wing area uses the length of the wing (distance between the shoulder and the tip of the wing) multiplied by the width obtained from the center of the extended wing. The tail area also uses length and width measurements. The aspect ratio was calculated as the square of the length of the extended wing divided by the wing area (Fitzpatrick 1986). I regressed wing and tail aspect ratios, and body size, a measure of wing and tail loading, (amount of body weight (gr) supported by unit area (cm^2) on DE. Wing and tail loading is an important determinant of flight performance (Gill 1990).

Breeding Biology

I used data on a species' annual breeding seasonality, clutch size, longevity, and generation time to estimate the intrinsic rate of natural increase using Cole's (1954) equation (See below). The length of the breeding season and clutch size of Amazonian

birds were estimated from nests found during surveys, from bird pets kept by the village residents, and from the literature. Nests were found along transects or by reports of local people on the location of active nests. Upon encounter, I recorded: species; clutch size at the moment of encounter; nest location; and date. Upon encounter with adults and their offspring, I recorded species; number of chicks; and date.

Information on wild bird pets also was used. In order to determine the breeding seasonality, I asked village residents that owned wild birds about: 1) the date of collection, 2) the time they have had the bird(s) as a pet, 3) the number of eggs/fledgling present at the moment of the capture, and 4) placement of the nest.

Intrinsic rate of population increase. Intrinsic rate of population increase (r_{max}) was calculated from Cole's (1954) equation. R_{max} was defined as the potential of a population for growth attained when the population is not limited by food or space. The equation uses information on reproductive parameters to generate an index of r_{max} by:

$$1 = e^{-\frac{r_{max}}{a}} + \frac{b e^{-r_{max}(w+1)}}{b e^{-r_{max}(w+1)}}$$

Where (a) is the generation time, (w) is the longevity, and (b) is the fecundity (annual birth rate of female offspring). Knowledge on longevity and generation time can be obtained almost solely through the bird banding process (Kelley 1993). These parameters were obtained from values published in the literature (See Tables). This study takes into consideration that data from captive-bred animals may not reflect actual parameters of wild animals (Lindstedt and Calder 1976). Thus, when possible, I used the mode or lower values from reports on captive populations. Fecundity was obtained by multiplying the minimum number of nesting attempts-year by 75% of a species average clutch size. Species that breed for a short period (three months) during an annual cycle

were assumed to have one nesting attempt. Species whose breeding seasons extended for longer periods of time were assumed to have 2 breeding attempts. Seventy-five percent was used to obtain the approximate number of female offspring-year assuming that 75% of pairs among Neotropical birds have one successful nest annually, a liberal estimate by Skutch (in Buckley et al. 1985).

Results

I quantified species' antipredator behavior, likelihood of detection and habitat use to test if these traits are associated with a disproportionate exposure to human hunting. Species differed in antipredator behaviors. Tinamous and wood-quails performed active antipredator strategies that consisted of explosive take off from the ground followed by a rapid and straight fly away from the observer. The DE was generally was over 25 meter (out of sight), and the average DE among species that performed this antipredator strategy was similar (Kruskal-Wallis $\chi^2=6.2$, $df=5$, $P=0.31$). Herons, ducks, anhingas and cormorants also performed active antipredator strategy and flew well over 25 meter upon reaction to hunters. An active antipredator behavior reduces the risk of human predation because it leaves hunters with little chance for a clear shot in both interior forest and in open habitats.

The semi-arboreal (Chapter 1) cracids, *M. tuberosa*, *P. jacquacu*, and *P. leucoptera*, and the arboreal macaws, parrots, toucans and *P. cumanensis* performed passive antipredator strategies upon reaction to hunters. Semi-arboreal species typically progressed away from the hunter by short gliding flights amidst branches or slowly walked away (*P. leucoptera*) on the forest floor remaining within shooting distance or

allowing hunters to ambush them and get a clear shot. Arboreal species either flew away or remained still in the forest canopy. DE varied among species that performed passive strategies (Kruskal-Wallis $\chi^2=21.1$, $df=3$, $P=0.000$), suggesting that the intensity of reaction differed among species that used passive evasive strategies (Figure 5-1).

Among interior forest species, active and passive antipredator behavior was linked to species' morphological traits. The relationship between body size and wing and tail morphology discriminated groups that performed stereotyped flights (Wilks' $\Lambda=0.21$, $\chi^2=11.3$, $df=5$, $P=0.05$) (Figure 5-2). A stepwise regression analysis using these three morphological traits and the species' average DE as dependent variable, revealed that wing shape and body size best explained the variation in DE (Table 5-1). Thus, the extent to which birds performed either short gliding flights (passive strategy) or fast and longer ones (active strategy). This analysis highlights the morphological basis of species antipredator behavior.

Table 5-1. Summary statistics for the multiple regression using DE as dependent variable and tail and wing aspect ratios, and body mass as predictors. Predictors represent a measure of wing and tail loading (wing and tail area/body weight) that is an important determinant of flight performance (Gill 1990).

	Coefficient	Standard error	t	P
Constant	-0.97	0.7	-1.39	0.25
Tail aspect ratio	0.28	0.13	-2.06	0.1
Wing aspect ratio	1.25	0.32	3.87	0.01
Body mass	0.4	0.11	-3.55	0.01

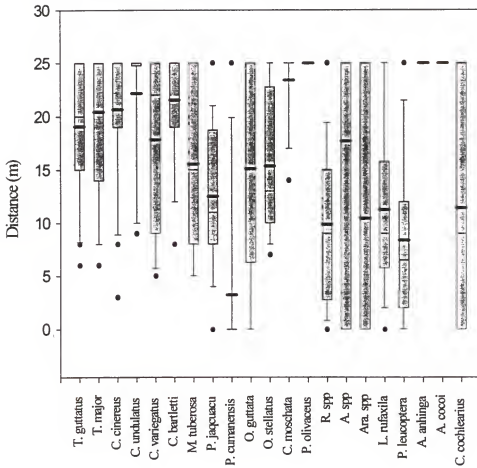


Figure 5-1 Distance of escape upon reaction to a hunter. Thick lines in box plot represent the mean, and thin lines the median with error bars and outliers (dots). The distance of escape differed among species (Kruskall-Wallis Test $\chi^2=250$, $df=20$, $P=0.000$).

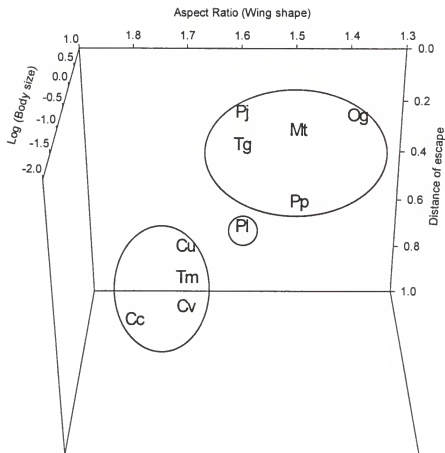


Figure 5-2. Relationship between morphological traits and species antipredator behavior. Species that perform passive antipredator behavior (upper circle) differ morphologically from those that perform active antipredator behaviors (bottom circle). Trumpeters (circle in the middle) represent an intermediate. Trumpeters use both, runs on the ground and flight to escape human predation. Species are represented by the following letters: Pj=Penelope jacquacu, Mt=Mitu tuberosa, Pp=Pipile cumanensis, Og=O. guttata, Pl=Psophia leucoptera, Cc=Crupturellus cinenerus, Cv=C. variegatus, Cu=C. undulatus and Tm= Tinamus major.

Probability of Detection

The frequency distribution of the distance of detection of *M. tuberosa*, *P. jacquacu*, and the trumpeter *P. leucoptera* were nearly twice the distance of detection of *Crypturellus spp.*, *Tinamus spp.*, *Leptotila rufaxila*, and *Odontophorus stellatus* (Figure 5-3). Among interior forest species the frequency distribution of the perpendicular distances of detection from the trail indicates that *M. tuberosa*, *P. jacquacu*, and *P. leucoptera* were more likely to be detected at distances than were significantly longer than other species (Table 5-2). During the field surveys, it was observed that *M. tuberosa*, *P. jacquacu*, and *P. leucoptera* gave cues (e.g., wing beats, foliage ruffle and vocalizations) that clearly lead.

Habitat Use.

P. cumanensis and *M. tuberosa*, were recorded at forest edges along permanent bodies of water (e.g., rivers and oxbow lakes) more often than away from them (Delacour and Amadon 1973, Hilty and Brown 1986, Stotz et al 1996, and Cox 1997, Ortiz and O'neil 1997) (Figure 5-4). The association with forest edges of permanent bodies of water appears to increase the chances that village residents encounter these species because most transportation is conducted via waterways and fishing is an important activity among riverine people. In addition, rural Amazonians carry a shotgun to most activities regardless of the main purpose to be ready for any opportunistic encounter with an animal. The kill site of *M. tuberosa* and *P. cumanensis* reported taken by hunters in upland and varzea forest show that 71% of individuals of the earlier species and 93%

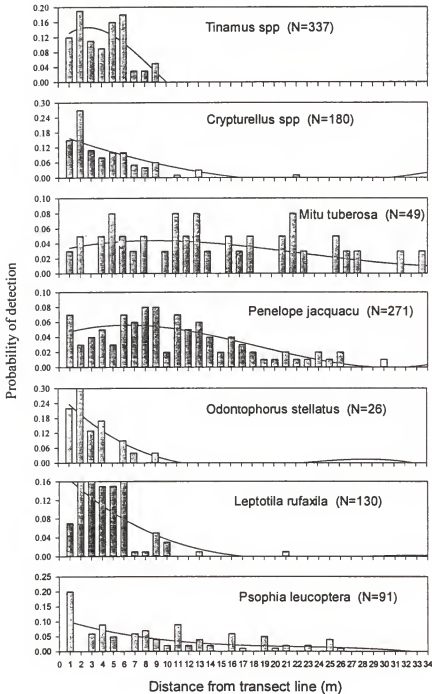


Figure 5-3. Probability that a hunter detects a bird prey at increasing distances from a trail. Cracids (*P. jacquacu*, *M. tuberosa*), and trumpeters (*P. leucoptera*) were more likely to be detected at longer distances than tinamous (*Tinamus* spp., *Crypturellus* spp.), Wood-quails (*O. stellatus*) and Doves (*L. rufaxila*).

Table 5-2. Summary statistics comparing the frequency distribution of the probability of detection from the observer provided in Figure (5-3). The procedure uses Kolmogorov-Smirnov test and significance at the 0.05 level.

	<i>Tinamus</i> <i>spp.</i>	<i>Crypturells</i> <i>spp.</i>	<i>Mitu</i> <i>tuberosa</i>	<i>Penelope</i> <i>jacquacu</i>	<i>Odontophorus</i> <i>stellatus</i>	<i>Leptotila</i> <i>rufaxila</i>	<i>Psophia</i> <i>leucoptera</i>
<i>Tinamus spp.</i>	1						
<i>Crypturells spp.</i>	0.45	1					
<i>Mitu tuberosa</i>	0.00	0.00	1				
<i>Penelope jacquacu</i>	0.00	0.00	0.43	1			
<i>Odontophorus stellatus</i>	0.38	0.62	0.00	0.00	1		
<i>Leptotila rufaxila</i>	0.29	0.63	0.00	0.00	0.05	1	
<i>Psophia leucoptera</i>	0.00	0.00	0.14	0.03	0.02	0.00	1

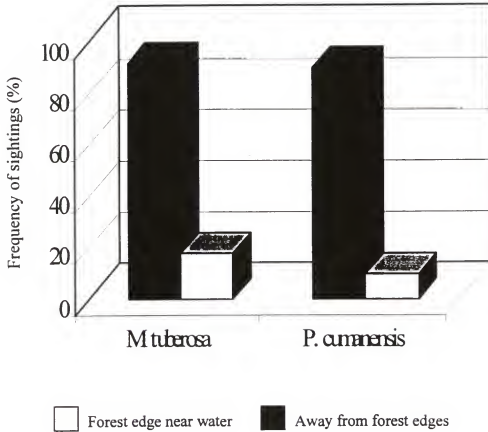


Figure 5-4. Habitat use by *M. tuberosa* (n=49) and *P. cumanensis* (n=120). Bars indicate the frequency of sightings (in percentage) at forest edges and away from forest edges. Data was obtained in both upland and varzea forest.

individuals of the later species were hunted near watercourses or permanent bodies of water, to detection at farther distances from the trail than the secretive *Crypturellus spp.*, *Tinamus spp.*, *Leptotila rufaxila*, and *Odontophorus stellatus* doves have an inconspicuous behavior and inhabit the forest floor. The size of species was positively correlated with longer distances of detection ($r=0.91$, $P=0.03$). These results suggest that a hunter will be more likely to detect cracids and trumpeters than doves, wood-quails and tinamous.

Predictors of Population Change from Hunting

Changes in population abundance. I examined the change in abundance (=individuals/100 km) of species by measuring the ratio of change between the unhunted and hunted sites. Species varied in the ratio of change of abundance. The mean ratio change of abundance among species in varzea forest (0.36) was greater than the mean ratio change of abundance in upland forest (0.06) ($t=2.4$, $df=16$, $P=0.02$) (Figure 5-5). Large cracids showed a more marked population decline in varzea forest than in upland forest. Trumpeters, and ducks declined in both forest types. Other species declined in one forest type but not in the other.

Group Size, Body Size, Position Within the Vertical Height of the Forest (PVF), and Relative Abundance

I used a multiple regression analysis to test if body size, group size, (PVF), and relative abundance in the unhunted sites (assumed to approximate the species carrying capacity) were predictors of the ratio of population change between unhunted and hunted

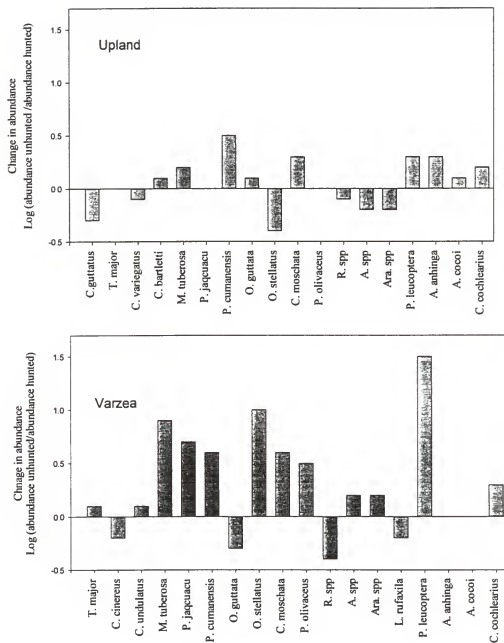


Figure 5-5. Changes in population abundance in upland and varzea forest. Positive numbers indicate increasing decline, whereas negative numbers indicate that populations were greater in the hunted sites than in the unhunted sites.

areas. In varzea forest, this analysis indicated that group size and body size were important predictors of the ratio of change of population decline (Table 5-3). In upland forest, a similar analysis showed that group size only was a good predictor of population decline at the $P=0.06$ level (Table 5-4).

Table 5-3. Summary statistics for the multiple regression with ratio of change in abundance between unhunted and hunted sites in varzea forest as dependent variable and group size, (PVF), body size and abundance (individuals/100 km) in the unhunted sites as independent variables.

Variable	Coefficient	Standard error	t	P
Constant	-0.58	0.68	-0.86	0.41
Group size	0.28	0.08	3.76	0.000
(PVF)	-0.01	0.01	-1.83	0.10
Body size	0.21	0.10	2.19	0.05
Abundance in unhunted sites.	0.00	0.03	-0.06	0.96

Table 5-4. Summary statistics for the multiple regression with ratio of change in population abundance in upland forest as dependent variable and group size, (PVF), body size and abundance (individuals/100 km) in the unhunted sites as independent variables.

Variable	Coefficient	Standard error	t	P
Constant	-0.10	0.15	-0.66	0.52
Group size	0.09	0.04	2.12	0.06
(PVF)	0.00	0.00	-0.59	0.56
Body size	0.05	0.06	0.95	0.36
Abundance in unhunted sites.	-0.02	0.01	-1.67	0.12

(PVF) was not a predictor of change in population size between the unhunted and hunted sites. The analysis of (PVF) indicates that most species, (72%, $n=18$) were regularly encountered within 10 meter of the ground. But hunting pressure did not correlate with species (PVF) in varzea forest ($r=0.26$, $P=0.31$) nor in upland forest

($r=0.02$, $P=0.9$). The ratio (Number of species/Number of individuals) hunted from above and below 10 meter was similar in varzea forest ($\chi^2=0.03$, $df=1$, $P=0.9$) and in upland forest ($\chi^2=0.2$, $df=1$, $P=0.6$), suggesting that (PVF) is a trait that does not lead to disproportionate hunting pressure.

Population abundance at equilibrium (=abundance in unhunted sites) was not a predictor of changes in population abundance between hunted and unhunted sites. Changes in abundance from hunting was illustrated in Chapter 4, where species of two large cracids and trumpeters showed the greatest population abundance in the unhunted sites and consistently the greatest decline in the hunted sites (Robinson and Wilcove 1989). Tinamous had smaller population abundance in the unhunted sites, and did not show changes in the hunted sites indicating differences in life history strategies where large standing population appear to be characterized by low reproductive outputs (Eisenberg et al 1979) and species that maintain lower populations by high reproductive outputs.

Breeding Biology

Breeding seasonality. I obtained species' reproductive parameters to estimate the intrinsic rate of increase (r_{max}). Subsequently, I examined changes in population abundance between the unhunted and hunted sites in terms of species' r_{max} . The Tinamidae either breed continuously or have long breeding seasons while *M. tuberosa*, *P. jacquacu*, *P. cumanensis*, *O. guttata*, *C. moschata*, *A. cocoli*, *C. cochlearius*, and *P. leucoptera* appear to breed in narrow breeding seasons (January-April) (Table 5-5).

Table 5-5. Evidence of breeding activity recorded during 1996-1998 in all sites in upland and varzea forest. Breeding records were also obtained from birds kept as pet by village residents in human settlements in upland and varzea forest.

	Eggs ^a	Chicks ^b	Date	Location	Long. (W)	Lat. (S)
Tinamidae						
<i>Tinamus guttatus</i>	4		12-Aug-97	Quebrada Blanco	73 06' 25.9"	04 23'37.5"
<i>Tinamus major</i>		3	Feb-97	San Pedro	73 11'53"	4 20'14.3"
<i>T. major</i>		4	Feb-98	San Pedro	73 11'53"	4 20'14.3"
<i>T. major</i>		1	July-97	Nueva Esperanza	75 05'47.9"	4 48'47.8"
<i>T. major</i>		4	Aug-97	Quebrada Armana	74 58'27.6"	05 00'08.2"
<i>T. major</i>		3	Aug-97	Quebrada Armana	74 58'27.6"	05 00'08.2"
<i>T. major</i>		3	Aug-97	Corrientillo	73 3'47.4"	4 23' 59.5"
<i>T. major</i>		2	Feb-97	Corrientillo	73 3'47.4"	4 23' 59.5"
<i>T. major</i>		3	Aug-97	Quebrada Armana	74 58'27.6"	05 00'08.2"
<i>T. major</i>	5		15-Mar-97	Lupunillo	73 6'25.9"	04 23'37.7"
<i>Crypturellus undulatus</i>	1		10-Jun-96	Yuracyacu	75 07'19"	05 13'34"
<i>C. undulatus</i>		2	Jun-96	San Pedro	73 11'59"	4 20'14.3"
<i>C. undulatus</i>	3		3-Jul-96	El Pinche	75 05'17.1"	04 51'13.3"
<i>C. undulatus</i>	2		19-Jun-96	Santa Elena	75 49'30.9"	05 14'04.5"
<i>C. undulatus</i>	2		19-Jul-97	El Pinche	75 05'17.1"	04 51'13.3"
<i>C. undulatus</i>	1		12-Jun-96	Santa Elena	75 49'30.9"	05 14'04.5"
<i>C. undulatus</i>	2		16-Aug-96	Nueva Esperanza	75 05'47.9"	4 48'47.8"
<i>C. undulatus</i>	3		16-Jun-96	Santa Elena	75 49'30.9"	05 14'04.5"
<i>Crypturellus cinereus</i>	1		1-May-96	Yuracyacu	75 07'19"	05 13'34"
<i>C. cinereus</i>		2	Jul-97	El Pinche	75 05'17.1"	04 51'13.3"
<i>C. cinereus</i>	2		2-Aug-97	El Pinche	75 05'17.1"	04 51'13.3"
<i>C. cinereus</i>	1		30-July-97	Quebrada Armana	74 58'27.1"	05 00'25"
<i>C. cinereus</i>	2		23-May-96	Yuracyacu	75 07'19"	05 13'34"
<i>C. cinereus</i>		1	Jun-96	Yuracyacu	75 07'19"	05 13'34"
<i>C. cinereus</i>	1		6-Aug-97	El Pinche	75 05'17.1"	04 51'13.3"
<i>Crypturellus bartileti</i>	2		25-Jun-97	Corrientillo	73 3'47.4"	4 23' 59.5"
<i>C. bartileti</i>	2		19-Jun-97	Corrientillo	73 3'47.4"	4 23' 59.5"
<i>Crypturellus variegatus</i>	2		14-Jun-97	Rio Mirin	72 24' 50.9"	04 30' 26"
<i>C. variegatus</i>	1		17-Feb-97	Corrientillo	73 3'47.4"	4 23' 59.5"
Cracidae						
<i>M. tuberosa</i>		2	Jan-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>C. mitu</i>		1	Feb-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>C. mitu</i>		1	Mar-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>C. mitu</i>		2	Apr-97	Buen Jardin	72 24'41.7"	04 31'14"
<i>C. mitu</i>		1	May-97	Pavaico	72 48'12.1"	4 40'32.3"
<i>C. mitu</i>		2	Jun-97	Carolina	71 47'40.6"	4 25'10.8"
<i>C. mitu</i>		1	Jul-97	Esperanza	71 51'04.9"	4 21'26.2"
<i>C. mitu</i>		2	Aug-97	Rio Mirin		
<i>C. mitu</i>		2	Sep-97	Esperanza	71 51'04.9"	4 21'26.2"
<i>Penelope jacquacu</i>		1	Oct-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>P. jacquacu</i>		2	Nov-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>P. jacquacu</i>		1	Dec-97	San Pedro	73 11'59"	4 20'14.3"
<i>P. jacquacu</i>		1	Jan-98	San Pedro	73 11'59"	4 20'14.3"

Table 5-5. continued

	Eggs ^a	Chicks ^b	Date	Location	Long. (W)	Lat. (S)
<i>P. jacquacu</i>		2	Mar-98	San Felipe	73 51'04.9"	6 21'26.2"
<i>P. jacquacu</i>		2	Apr-98	Buen Jardin	72 24'41.7"	04 31'14"
<i>P. jacquacu</i>		1	May-98	Quebrada Blanco	73 7' 35.0"	04 23'3.6"
<i>P. jacquacu</i>		1	Jun-98	Quebrada Blanco	73 7' 35.0"	04 23'3.6"
<i>P. jacquacu</i>		3	Jul-98	Pavaico	72 48'12.1"	4 40'32.3"
<i>P. jacquacu</i>		1	Aug-98	Pavaico	72 48'12.1"	4 40'32.3"
<i>P. jacquacu</i>		2	Sep-98	Pavaico	72 48'12.1"	4 40'32.3"
<i>Ortalis guttata</i>		3	Oct-98	Maipuco	75 07' 01.0"	04 49' 17.7"
<i>O. guttata</i>		1	Nov-98	Maipuco	75 07' 01.0"	04 49' 17.7"
<i>O. guttata</i>		2	Dec-98	Nueva Esperanza	75 05'47.9"	4 48'47.8"
Psittacidae						
<i>Amazona spp</i>		2	March	Rio Marañom	c	
<i>Amazona spp</i>		1	March	Rio Marañom	c	
<i>Ara spp</i>		1	Feb	Rio Marañom	c	
<i>Ara spp</i>		1	March	Rio Marañom	c	
Anatidae						
<i>Cairina moschata</i>		5	Mar-97	Rio Samiria	75 49'30.9"	05 14'04.5"
Pelecanidae						
<i>Phalacrocor. olivaceus</i>		2	March	Pac-Sam Area	CDC 1993, Soini 1990.	^d
<i>Anhinga anhinga</i>		2	March	Pac-Sam Area	CDC 1993, Soini 1991.	^d
Ardeidae						
<i>Ardea cocoi</i>		3	March	Pac-Sam Area	71 51'04.9"	4 21'26.2"
<i>Cochlear. cochlearius</i>		1	March	Pac-Sam Area	75 07' 01.0"	04 49' 17.7"
Psophiidae						
<i>Psophia leucoptera</i>		3	Feb-97	Quebrada Blanco	73 06' 25.9"	04 23'37.5"
<i>P. leucoptera</i>		2	Feb-97	Quebrada Blanco	73 06' 25.9"	04 23'37.5"
<i>P. leucoptera</i>		2	Mar-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>P. leucoptera</i>		2	Apr-97	San Felipe	71 51'04.9"	4 21'26.2"
<i>P. leucoptera</i>		1	Feb-97	Pavaico	72 48'12.1"	4 40'32.3"

^a Nests found during this study.^b Chicks observed in the forest and birds kept by village residents.^c Birds being transported for sale in the city market.^d References used to document breeding biology of species in the study.

Studies provided further support for this observation. Magalhães (1972), cited in (Sick 1993), reports that 8 species of forest tinamous (*Tinamus* and *Crypturellus*) between the latitudes of 10°S and 13°S had a peak in nesting frequency during the onset of the rainy season (December- January) and decreased, but continued for over 6 months of the year. Leopold (1959) also reported breeding periods that lasted 4–6 months for Mexican tinamous of the same genera. In contrast, the cracids (Franco and Santa Maria 1997), trumpeters (Sherman 1995), ducks and herons (Soini 1990), toucans, macaws and parrots (Hilty and Brown 1986, Forshaw 1973) appeared to breed in a relatively short and fixed seasons.

Clutch size. Species' average clutch size ranged from 1.5 to 9.1 eggs (Table 5-6). Among species hunted more frequently, the average clutch size varied as follows: Ducks 9.1 ± 1.2 , ($n=6$), trumpeters 4 ± 0.8 , ($n=7$), tinamous 3.1 ± 1.8 , ($n=55$), herons 2.9 ± 0.5 , ($n=11$), cracids 2.5 ± 0.7 , ($n=69$), and macaws and parrots 2.2 ± 1.2 , ($n=17$) ($df=2$, $F=9.29$, $P<0.000$). Among the Tinamidae, species of the genus *Tinamus* had larger average clutch sizes, 5.04 ± 1.2 ($n=21$), than those of the genus *Crypturellus* 1.8 ± 0.71 ($n=34$). Among the Cracidae, *O. guttata* had the largest clutch size followed by *P. cumanensis*. *P. jacquacu* and *M. tuberosa*.

Intrinsic rate of population increase (r_{max}). I examined species' r_{max} to see its implications on changes in population abundance from hunting. R_{max} values ranged from 0.46 to 1.46 (Table 5-7). The average r_{max} differed among the Tinamidae ($n=6$ species), Anatidae ($n=1$ species), Ardeidae ($n=2$ species), Psittacidae ($n=2$ species), Cracidae ($n=4$ species), and Psophiidae ($n=1$ species) ($F=78$, $df=2$, $P<0.000$) (Figure 5-6). Species' with low r_{max} showed greater rates of decline and this was consistent

Table 5-6. Clutch size of species treated in this study. Data on clutch size was obtained from nest found in the upland and varzea forest study sites during 1996-1998, published literature and from information obtained from village residents on eggs collected chicks trapped and raised as pet.

	Mean	Mode	Median	Range	SE	N ^a	95% C L	Position ^b	References ^d
<i>Tinamus guttatus</i>	4.25	4	4	3-6	0.31	8	0.61	G	3, 7, 11, 15
<i>Tinamus major</i>	5.53	6	6	4-7	0.29	13	0.57	G	3, 4, 7, 11, 15
<i>Crypturellus cinereus</i>	1.5	1	1.5	1-2	0.19	8	0.37	G	7, 15
<i>Crypturellus undulatus</i>	2	1	2	1-3	0.24	12	0.48	G	7, 11, 15
<i>Crypturellus variegatus</i>	1.7	2	2	1-2	0.18	7	0.36	G	3, 8, 11, 15
<i>Crypturellus bartleti</i>	2	2	2	1-3	0.3	4	0.6	G	3, 7
<i>Mitu tuberosa</i>	2	2	2	2-2	0	25	0.00	A	1, 2, 5, 6, 7, 11, 12, 13, 15
<i>Penelope jacquacu</i>	2.47	2	2	2-3	0.11	21	0.21	A	1, 2, 7, 11, 12, 16.
<i>Pipile cumanensis</i>	2.57	3	3	2-3	0.2	7	0.39	A	1, 2, 7, 11, 15.
<i>Ortalis gutatta</i>	3.4	4	3.5	2-4	0.16	16	0.31	A	1, 2, 7, 15.
<i>Odontophorus stellatus</i>	3.75	3	3.5	3-5	0.48	6	0.93	G	7, 15
<i>Cairina moschata</i>	9.1	8	9	8-11	0.47	6	0.93	C	7, 8, 9, 11, 15,
<i>Phalacrocorax olivaceus</i>	2.8	3	3	2-3	0.2	5	0.39	A	7, 11, 15.
<i>Ramphastos spp</i>	2	2	2	1-3	0.31	3	0.61	C	7
<i>Amazona spp</i>	2.5	3	2.5	2-3	0.22	6	0.43	C	7, 15
<i>Ara spp</i>	1.83	2	3	1-2	0.16	6	0.33	C	7, 15
<i>Leptotila rufaxila</i>	2	2	2	2-2	0	5	0.00	A	7, 15
<i>Psophia leucoptera</i>	4	4	4	3-5	0.3	7	0.6	C	7, 14, 15
<i>Anginã aninga</i>	2.71	3	3	1-2	0.18	7	0.36	A	7, 8, 11, 15
<i>Ardea cocoi</i>	3.2	3	3	3-4	0.2	5	0.39	A	7, 8, 11, 15
<i>Cochlearius cochlearius</i>	2.75	3	3	2-3	0.25	4	0.48	A	7, 8, 11, 15

^a Includes field records obtained in this study and data from the literature.

^b Position of nest. G=Ground, A=Arboreal and C=Cavity.

^d References: 1=Delacour and Amadon 1973; 2=Estudillo-Lopez 1988; 3=Euler 1900 cited in (15); 4=Forti and Vispo (In Press); 5=Franco and Santamaria 1997; 6=Gutierrez 1997; 7=Hilty and Brown 1986; 8=Leopold 1959; 9=Madge and Burn 1988; 10=Ollson 1977; 11=Soini 1990; 12=Schifter 1989; 13=Sermeño 1997; 14=Sherman 1995; 15=Sick 1993; 16=Tello and Pedraglio 1997; 17=Begazo 1996.

Table 5-7. Reproductive parameters used to estimate species intrinsic rate of population increase (r_{max}). R_{max} was estimated using Cole's (1956) equation.

	a	b	w	r	
	Age of first reproduction	Annual birth rate	Age of last reproduction	r_{max}	References
<i>Tinamus guttatus</i>	1.5	4.87	10	1.27	1, 5, 10, 18.
<i>Tinamus major</i>	1.5	4.87	10	1.27	1, 5, 10, 18.
<i>Crypturellus cinereus</i>	1	3	10	1.4	1, 5, 10, 18.
<i>Crypturellus undulatus</i>	1	3	10	1.4	1, 5, 10, 18.
<i>Crypturellus variegatus</i>	1	3	10	1.4	1, 5, 10, 18.
<i>Crypturellus bartletti</i>	1	2	10	1.09	1, 5, 10, 18.
<i>Mitu tuberosa</i>	3	1.5	24	0.46	2, 3, 10, 14, 16, 18, 19, 20.
<i>Penelope jacquacu</i>	3	2.25	20	0.55	2, 10, 18, 19, 20.
<i>Pipile cumanensis</i>	3	2.25	20	0.55	2, 3, 18, 19, 20.
<i>Ortalis gutatta</i>	2.5	2.62	20	0.67	2, 3, 10, 12, 18, 19.
<i>Odontophorus stellatus</i>	1	1.87	14	1.05	19.
<i>Cairina moschata</i>	2	8.62	12	1.25	7, 10, 11, 18.
<i>Phalacrocorax olivaceous</i>	2	2.1	15	0.7	8, 18.
<i>Ramphastos spp</i>	2	2.25	15	0.73	18.
<i>Amazona spp</i>	2	2.25	20	0.73	5, 13, 18.
<i>Ara spp</i>	2	1.5	20	0.6	5, 13, 18.
<i>Leptotila rufaxila</i>	1	1.5	12	1.25	15.
<i>Psophia leucoptera</i>	3	1.2	15	0.42	17, 18.
<i>Anginha anhinga</i>	2	2.25	15	0.73	8, 18.
<i>Ardea cocoi</i>	2	1.87	15	0.67	6, 18.
<i>Cochlearius cochlearius</i>	2	1.87	15	0.67	6, 18.

1=Aguirre 1959; Cited in (Coimbra-Filho 1971); 2=Delacour and Amadon 1973; 3=Estudillo-Lopez 1988; 4=Forshaw 1973; 6=Hancock and Kushlan 1984; 7=Johnsgard 1978; 8=Johnsgard 1993; 9=Juniper 1998; 10=Leopold 1959; 11=Madge and Burn 1988; 12=Marion and Raymond 1978; 13=Munn 1992; 14=Ollson 1977; 15=Lindstedt and Calder 1976; 16= Schifter 1989; 17=Sherman 1995; 18=Sick 1993; 19=Silva and Strahl 1991; 20=Strahl and Silva 1997.

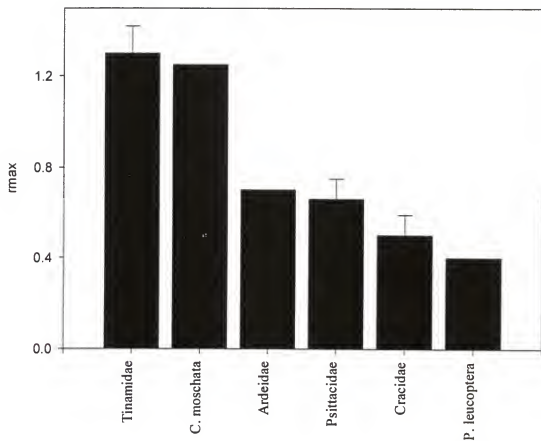


Figure 5-6. Variation in r_{max} values among the most commonly hunted taxa. Tinamous and trumpeters represent the highest and lowest values.

in upland and varzea forest, (Figure 5-7) suggesting that r_{max} is an important determinant of population decline (Bodmer 1997). A general linear model using reproductive parameters and r_{max} indicated that generation time, and fecundity best explained the variation in r_{max} (Table 5-8). This suggests that, among Amazonian birds hunted by humans, species with short generation time and high rates of fecundity have high intrinsic rates of population growth, while species that take longer to attain sexual maturity have low fecundity and low rates of population growth.

Table 5-8. Summary statistics for the regression analysis using r_{max} as independent variable and reproductive parameters as predictors.

Variable	Coefficient	Standard Error	t	P
Constant	1.5	0.1	11.8	0.000
Age of first reproduction	-0.3	0.1	-5.3	0.000
Female/offspring/year	0.1	0.0	4.2	0.001
Age of last reproduction	0.0	0.0	-1.2	0.257

Body size showed important associations with fecundity, generation time, and longevity. Body size was correlated to generation time ($r=0.7$, $P=0.001$), and longevity ($r=0.8$, $P<0.000$), but not with fecundity ($r=-0.2$, $P=0.4$). These results suggest that body size is a determinant of sexual maturity and life span, but not of annual reproductive output. Finally, body size was negatively correlated with r_{max} , suggesting that reproductive productivity was lower among large birds and higher among small

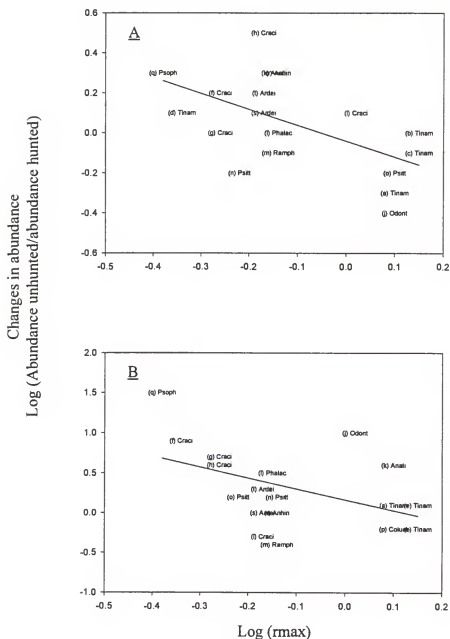


Figure 5-7. Relationship between the vulnerability of birds to population decline measured as the change in abundance between the unhunted and hunted sites and rmax. **A** represents upland forest ($r = -0.6$, $P = 0.01$), and **B** varzea forest ($r = -0.5$, $P = 0.06$). The species are represented by the following letters, a=T. Major, b=T. Major, c=C. variegatus, d=C. bartletti, e=C. undulatus, f=M. tuberosa, g=P. jaquacu, h=P. cumensis, i=O. guttata, j=O. stellatus, k=C. moschata, l=P. olivaceous, m=Ramphastos spp., n=Amazona spp., o=Ara spp., p=L. rufaxila, q=P. leucoptera, r=A. Anhinga, s=A. cococi, t=C. cochlearius.

birds (Figure 5-8).

Ecological Relationships Among Species

Changes in abundance between unhunted and hunted populations appears not to occur randomly. Ratio of change in population abundance was associated with ecological traits to varying extents (Table 5-9). The test of hierarchical cluster analysis (SPSS 1996), grouped tinamous and trumpeters in a group and all cracids in a separate group (Figure 5-9). While tinamous and trumpeters are ecologically similar, both groups differ in their reproductive biology, which appears to be an important correlate of population decline. The cracids are also species ecologically similar. However, *O. guttata* is smaller and appears to have greater rates of population increase that help explain the low hunting pressure, and perhaps the better capacity of population recovery than other cracids.

Discussion

A primary goal of conservation biology is to provide principles and practices by which biological diversity can be conserved in the face of anthropogenic impact (Soulé 1985). After habitat destruction, overhunting represents the most common cause of species extinction (Reid 1992). But extinction is rarely cataclysmic. Rather, it is a progressive process with total extinction preceded by local and regional population decline (Caughley and Gunn 1996). Thus, determining the ecological correlates of population decline can provide insights into pinpointing potential species in danger of extinction. In addition, determining the correlates of population decline may help develop general principles

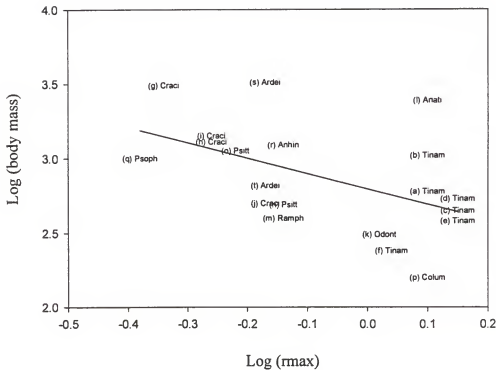


Figure 5-8. Relationship between the size and each species' intrinsic rate of natural increase, r_{max} ($r = -0.51$, $P = 0.002$). The species are represented by the following letters, a=T. guttatus, b=T. major, c=C. variegatus, d=C. bartletti, e=C. undulatus, f=M. tuberosa, g=P. jaquacu h=P. cumanensis, i=O. guttata, k=O. stellatus, l=C. moschata, L=P. olivaceous, m=Ramphastos spp, n=Amazona spp., o=Ara spp., p=L. rufaxila, q=P. leucoptera, r=A.Anhinga, s=A. cococi, t=C. cochlearius.

Table 5-9. Ratio of change between unhunted and hunted populations, and associated ecological traits. Ratio of change is given in ascending order (negative values indicate that populations in hunted sites were greater than those in unhunted sites). Values for each ecological trait were divided into three categories, low (light gray), medium (medium gray), and high (dark gray). The three categories represent values between the smallest and largest values recorded for each trait. Values between the smallest and largest value were obtained using an automatic scaling that takes the ratio of increase from value to value in the data set. Then, all values within the range of values were divided into three categories. Subsequently, each value from the actual data set was placed within each of the three ranges of values accordingly. This procedure was repeated for each trait.

Species	Ratio of population change Unhunted/hunted	Average group size	Average position along the vertical length of the forest	Size (kg)	rmax	Distance of escape	Distance of detection	Wing loading	Tail loading
<i>Tinamus guttatus</i>	0.23	1.0	0	1.6	1.3	0.5	4.66	1.9	40
<i>Ortalis guttata</i>	0.19	1.0	21	0.5	0.67	0.4	9	0.9	33.4
<i>Crypturellus cinereus</i>	0.19	1.1	0	0.5	1.4	0.7	4.36	1.7	45
<i>Crypturellus variegatus</i>	0.11	1.1	0	0.4	1.4	0.5	4.76	2.6	68.6
<i>Tinamus major</i>	0.08	1.1	0	1.1	1.5	0.2	4.66	2.5	63.8
<i>Crypturellus bartletti</i>	0.11	1.2	0	0.3	1.09	0.7	4.36	3.3	96.4
<i>Crypturellus undulatus</i>	0.11	1.1	0	1.5	1.4	0.8	4.36	1.8	47
<i>Pipile cumanensis</i>	0.6	2.9	38.7	1.4	0.55	0.1	14	1.5	4.9
<i>Penelope jacquacu</i>	0.7	1.8	2.7	1.3	0.55	0.2	10.06	1.2	31.6
<i>Mitu tuberosa</i>	0.9	1.5	2.6	3.1	0.46	0.3	13.41	1.5	7.8
<i>Psophia leucoptera</i>	1.5	6.5	0	1	0.12	0.1	8.52	1.2	44

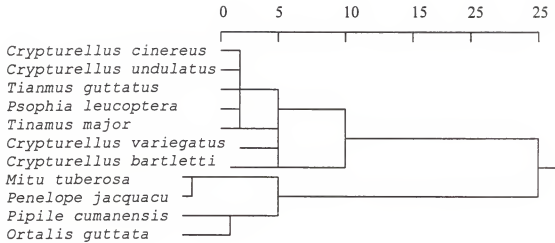


Figure 5-9. Ecological correlates among Amazonian birds more frequently hunted. The analysis distinguishes two groups. Notice that *P. leucoptera* was grouped with *Tinamus*. Except for differences in reproductive biology (represented by *rmax*), this species is ecologically more similar to tinamous than curassows (*M. tuberosa*), guans (*P. jacquacu*, *P. cumanensis*) and chachalacas (*O. guttata*). The hierarchical cluster analysis performed on 9 variables measured on 11 species identifies groups of cases (species) based on measured characteristics on such cases. Distance or similarity measures are generated by the proximities procedure using the average linkage between groups (SPSS 1996). To test the model of group membership I used a discriminant analysis (Wilks' Lambda=0.002, Chi-square=27.3, df=9, P=0.001) using the two groups of membership generated by the previous analysis. Discriminant analysis is based on linear combinations of the predictor variables which provide the best discrimination between groups (SPSS 1996).

through which managers can direct their effort when addressing the use and conservation of Amazonian wildlife.

Distance of Detection and Antipredator Behavior

The analysis of a species' antipredator behavior, likelihood of detection and habitat use leads to the interpretation that some species are more vulnerable than others to hunters. Testing this interpretation would require quantifying the outcome of actual encounters between hunters and birds. Such data were not available. Instead, I use the current harvest and avian community structure to infer the influence of distance of detection and antipredator behavior on the disproportionate exposure to human hunting.

Populations of *M. tuberosa*, *P. jacquacu*, *P. cumanensis* and *P. leucoptera* showed the traits that result in a greater exposure to hunting and declined predictably in upland and varzea forest ecosystems. On the hunting grounds near the settlement in varzea forest, these species have been locally extirpated or became very rare. In upland forest all of these species experienced the greatest population decline. In addition, a greater population decline from hunting among populations of these species is consistent in a wide range of situations (Delacour and Amadon 1973, Estudillo-Lopez 1988, Strhal and Grajal 1990, Silva and Strhal 1991). Furthermore, species that have the behavioral traits that lead to greater exposure to hunting are more frequently harvested than others. In conditions where all species were available (e.g., grounds searched in long trips), hunters took species expected to be taken at greater rates than species that did show traits that expose them to disproportional hunting (Chapter 3).

In addition to differences in antipredator behavior, species body size and average group size might also be traits that lead to disproportional hunting, and they were the best predictors of population decline. Hunters preferred birds that were large and gregarious. Greater preference and population decline among large and gregarious birds can be better understood by linking these variables to hunting patterns of Amazonian hunters. Selecting large and gregarious birds makes sense, because hunters obtain more meat per ammunition (Redford 1992, Hawkes et al 1997), and can potentially make multiple kills by killing the target birds and adjacent individuals, and by continuous pursuit of the group (Peres 1990, Fitzgibbon et al 1996).

Variation in species social structure is likely to influence population decline from hunting. Cracids maintain permanent pairs or are regularly found in family groups (Shifter 1988, Franco and Santamaria 1996). Trumpeters live in groups of complicated social dynamics (Sherman 1995). On the other hand tinamous have polyandric mating system known not known to form permanent pairs (Sick 1993). Therefore, it is likely that among cracids and trumpeters, hunting not only removed individual from the population, but also disrupted the social structure and the population dynamics (Buccher 1992).

Group size was a predictor of change in population from hunting. Theory predicts that the optimal group size is a direct response to the constraints of food finding and early detection of predator (Balmford and Turyaho 1992, Janson 1992). However, early detection of a human predator by gregarious birds resulted in cues (e.g., movements and emission of alarm calls) that led to detection by hunters. Stanford (1995) in a comparative study, suggested that a possible evolutionary response of Colobus Monkeys,

Ptilocolobus badius, to minimize the risk of detection and predation by Chimpanzees, *Pan troglodytes*, was the reduction of group size and the suppression of movements and vocalizations when aware of the presence of chimpanzees. Hunters use visual and audio cues to locate prey. Therefore inherent behavioral traits may represent an initial maladaptation to predation by humans (Milberg and Tyrberg 1993).

Group size and territorial habits may also determine the way in which hunting influences species. For example cracids and trumpeters live in larger groups which occupy permanent territories (Sherman 1995, Franco and Santamaria 1996). Therefore, it is possible that hunters drive populations to local extinction by eliminating a few groups established in territories within the catchment area. On the other hand, tinamous maintain smaller territories and live individually (Forti and Vispo In press). As a result hunting may not influence tinamous populations as greatly as those of cracid, and trumpeter populations.

Reproductive Biology.

Having discussed traits that are associated to disproportional hunting pressure, I discuss the biological mechanisms of population declines from hunting. The intrinsic rate of population increase indicates the capacity of population for growth (Lotka 1925). A high r_{max} results from many offspring, large clutches, multiple broods, short generation time, and a long reproductive life. The results obtained in this study concur with the notion that species can be arranged in a fast-slow continuum with species ranging from those with high birth rate, high rates of development and short lives to those with low birth rates, low rates of development and long lives (Ross 1992).

Species with lower r_{max} , longer-lived, and long generation time were associated with greater rates of population decline than species with high r_{max} , short-lived and short generation time. Lower r_{max} , long generation time and long life span were associated with larger birds. The implications of r_{max} , generation time and longevity and size on population decline can be better understood by considering their links with recruitment. Removing individuals of species with long generation times and long life spans would have a greater impact on the population recruitment than removing individuals with short generation times and short live span (Fitzgibbon et al 1996, Alvard et al. 1997, Bodmer et al. 1997). This pattern was observed in this study. Among large species, the cracids and trumpeters were both more exposed to hunting, consistently selected by hunters and showed greater decline. While large and small tinamous were also preferred by hunters they were less exposed to hunting and better able to compensate for hunting.

Mating system. As part of the analysis of reproductive biology, I provide a review of species' mating systems obtained from published literature. Tinamous (Leopold 1959, Sick 1993) and the duck *C. moschata* (Johnsgard 1978) have polygamous mating systems that favor high reproductive outputs (Brewer and Swander 1977). Cracids (Delacour and Amadon 1973, Franco and Santamaria 1997, Estudillo- Lopez 1988), trumpeters (Sherman 1995), and herons (Hancock and Kushlan 1984) have a monogamous breeding system that favors lower reproductive outputs (Brewer and Swander 1977).

Tinamidae have a polyandric mating system. Females of the genus *Tinamus* can lay up to 3 simultaneous clutches of 3-6 eggs on nests of three separate males (Aguirre 1959, cited in Coimbra-Filho 1971). Females of the genus *Crypturellus*, can lay up to 5

clutches of 1-3 eggs on nests of separate males, and males may sit on a new clutch while still taking care of semi-independent young (Euler 1900, cited in Sick 1993). With birds maintained in an enclosure, the tinamid *Rynchotus rufescens* laid 30 eggs, but only two males incubated them, suggesting that in the wild these eggs might have been laid on the nest of separate males (Sick 1993). Moreover, females of the later species have been reported to lay up to 85 eggs in 4 months after the eggs were removed (Sick 1993).

The monogamous cracids, trumpeters, herons parrots macaws and toucans appear to have less prolific reproductive traits. In a 5-year study of a wild habituated pair of curassows (*Mitu salvini*), 3 chicks hatched and were successfully raised by the parents. The chicks remained with the parents for 10 months before they became independent. Moreover, the pair attempted to breed every year but curtailed attempts when nest predation occurred near the end of the breeding season (Franco and Santamaría 1997). Trumpeters have monogamous and cooperative breeding system where only 1 pair of a group of 7 individuals on average breeds every year. In addition, trumpeters have small broods, short and seasonal breeding activity and long parental care (Sherman 1995). Amazonian herons raise a single brood, but the extent to which birds bred is linked to adequate water levels with years of little breeding activity during abnormal years (Soini 1990).

Current ecological pressures on species provide insights into understanding differences in vulnerability to population decline (Balmford 1996). In forest conditions, predation influences mortality and species with high mortality rates must have high natality rates, therefore, a high r_{max} (Robinson and Redford 1986). Since high natality rates are associated to high r_{max} , then it would be expected that mortality is high among

ground dwelling species (e.g., tinamous), and low among arboreal and semiarboreal species (e.g., cracids and trumpeters). Species specific mortality rates calculated from field studies are generally lacking. However, tinamous might be subject to greater rates of mortality. Most species of Amazonian tinamous roost on the forest floor (personal observation), and all species forage and nest on the ground (Murray 1992, Martin 1996). Arboreal and semiarboreal species are probably less vulnerable to predators than ground dwelling birds because arboreality allows animals to avoid at least the most terrestrial predators (Devore and Hall 1965).

Variation in r_{max} could be traced to past ecological pressures. Morphological, behavioral, and reproductive biology among forest tinamous are similar to taxonomically related tinamous that inhabit open habitats (e.g., savanna, grasslands). These affinities suggest that forest tinamous might have evolved in open habitats and later colonized forested habitats. Open habitats are considered unstable environments, and species inhabiting such habitats frequently show life history traits favoring high r_{max} (e.g., large clutch size, multiple broods and polygamous mating systems) (Brewer and Swander 1977, Ross 1992). Thus, it is reasonable to infer that unstable environments shaped reproductive traits of the tinamous that after colonizing forested habitats faced an equally unstable environment in the form of high rates of mortality associated to life on the forest floor and periodic inundation's among species restricted to life in varzea forest. Conversely, cracids and trumpeters typically inhabit forested areas and their reproductive traits fit those suggested for species that have evolved in stable environments that favor low r_{max} (Lack 1968, Fodgen 1972). Hence, mortality from hunting may not influence

populations of the tinamous, because species are able to cope with novel changes if they have been exposed to similar challenges in their evolutionary history (Sieving 1992).

Auxiliary evidence helps explain the implications of behavioral and biological traits on population decline from hunting. The cracid nocturnal curassow (NC) (*Nothrocax urumutum*) has similar body size (1.3 kg), morphology and reproductive parameters as *M. tuberosa*, *P. jacquacu*, and *P. cumanensis*, but differs in its antipredator behavior. NC are extremely secretive, remaining motionless when aware of human presence, or run on the ground taking to the trees as means to avoid predation only in situations of high threat (when chased by hunting dogs) (Delacour and Amadon 1973). Field surveys suggest that the species is not heavily hunted and persists in areas where other species of cracids have been locally extirpated (J. P. O'Neil personal communication).

A contrasting case is the Wattled curassow (*Crax globulosa*). Wattled curassow resembles *M. tuberosa* in most traits but is more gregarious being found in groups of 6-30 individuals. Conspicuous behavior, and gregarious habits that resulted in multiple kills upon encounter of a group (comments from elders in the villages) may have driven the species to its current threatened status (Statterfield et al. 1998).

Population decline from hunting does not occur randomly, but appears to be associated with species that combine naïve antipredator behavior, are easily detected by hunters are large, live in groups, and have low rates of r_{max} . While this study identifies associations between ecological traits with population decline from hunting, the relative importance of each factor in determining population decline needs further testing.

CHAPTER 6

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

In this dissertation, I examined the hunting of Amazonian birds and its association with their population abundances, as well as the proximate factors of population decline from hunting. Bird hunting was studied in two areas that encompassed the major landscape characteristics (upland and varzea forest) and the socio-economic features (riverine culture) of the Peruvian Amazon. Bird hunting was examined on the premise that upland and varzea forest represent two ecologically different forest ecosystems (Encarnacion 1993, Gentry 1988, Pires and Prance 1987) that influence the occurrence and abundance of wildlife (Janzen 1974, Emmons 1984, Peres 1996b) and the activities of ribereño people (FPCN 1994).

Upland and varzea forests are ecologically different. Upland forest is not subject to seasonal floods, fruit is less available, and it is likely to have a greater invertebrate biomass on the forest floor. Varzea forest is subject to seasonal floods, greater fruit production and lower leaf litter cover, that is likely to result in lower invertebrate abundance in the forest floor (Chapter 2). Most species (75%) examined in this study eat fruit to varying degrees (Redford et al 1992, Chapter 3), and abundance of food resources often correlates with abundance of animals (Howe et al 1983, Levey 1988, Loiselle and Blake 1991). However, the occurrence and abundance of frequently hunted Amazonian bird species seemed not be associated with ecological differences. Moreover, 2-4-month long seasonal floods appeared not to influence population abundances of Amazonian

birds. Half of all species (50%) use the forest floor to varying degrees. Population abundance among ground users was also similar between forest types, varying at the individual species level. Population abundance of Amazonian birds appeared not to concur with the most obvious ecological differences (seasonal floods, variation in soil quality, and variation in productivity) that have been used to explain variation in population abundance between upland and varzea forest (Janzen 1974, Emmons 1984, Bodmer 1990, and Peres 1996b). However, auxiliary information suggests that seasonal floods may be responsible for temporal fluctuations in population abundance of at least the most terrestrial birds (e.g., tinamous) in varzea forest.

The impact of hunting on Amazonian birds appeared to be linked to differences in human population densities, age of the settlement, and settlement patterns. Hunters preferred large birds that had "good meat", but took most any bird that was available on the hunting grounds. The current availability of birds to hunters was determined by the impact of past hunting on bird populations. Hunting did not equally influence the population abundance of Amazonian birds. The large cracids *M. tuberosa*, *P. cumanensis*, *P. jacquacu* and the trumpeter *P. leucoptera* showed the greatest population abundance in the control sites, but experienced among the greatest decline in the hunted sites (Robinson and Wilcove 1989). In contrast, populations of the tinamous and the small cracid *O. guttata* had lower populations in the control sites and did not show changes in population abundance from hunting. This result suggests that species rates of population increase were more important than standing population sizes in determining rates of recovery (Eisenberg et al 1979), and changes in population abundance from hunting. Among large cracids and trumpeters, hunting was associated with greater

changes in population abundances and local extirpation in varzea forest than in upland forest, in spite of the fact that birds were taken at greater rates in upland forest.

Characteristics of human settlements, rather than ecological differences in forest type, help explain this result. The village of San Pedro in upland forest is a younger human settlement, less densely populated, households are spread along 24 km stretch of meandering river, and hunt in larger catchment areas at the rate of one consumer/5.4 km². The village of Nueva Esperanza, in varzea forest, is an older settlement, more densely populated, concentrated around a central place, and uses a smaller catchment area at the rate of one consumer/2 km². Hunting pressure spread over large areas is more likely to allow harvested population to compensate for individuals removed from the population (MacCullough 1996). Finally, the available data did not show that species that inhabit open habitats were influenced by hunting. These species typically spread over large areas in search of often ephemeral sources of food (e.g., fruit and fish) (Snow 1981, Levey and Stiles 1992, Munn 1994). Birds from areas may be moving into the catchment areas sampled making detection of the influence of hunting difficult (Novaro 1995, Peres 1996a).

The analysis of sustainability of bird hunting indicates that some species are being overhunted, others are being hunted at population sizes that may not be sustainable in the long term, and other are being harvested sustainably. The harvest and production models indicate that *Ara spp.* and *M. tuberosa* in varzea forest and *P. cumanensis* in upland forest are being hunted at rates that surpass the species annual production. Moreover, the stock-recruitment model suggested that current harvest of 7 species (39%) in upland forest and 6 (28%) in varzea forest falls below the predicted maximum sustainable yield (MSY),

therefore hunting may be driving these populations to local extinction. Accepting the data, the harvest of species that are below the predicted MSY should be lowered so that populations can increase to level above the MSY.

Species that showed population declines associated with hunting appeared to be ecologically different from others. Inefficient antipredator behaviors, greater likelihood of detection, and habitat use seemed to expose large cracids and trumpeters to a greater hunting pressure. Moreover, body size and group size were predictors of population decline and hunters selected large and gregarious birds, that characterize cracids and trumpeters. Species more exposed to hunting were taken more frequently in situations where all species were available to hunters (e.g., distant hunting grounds), and consistently showed a greater population decline than others. There were biological mechanisms that explained patterns of population decline observed. Hunters preferred large species and trumpeters, but they are also the most susceptible to population decline because of lower rates of intrinsic increase, increased longevity and longer generation time. Conversely, hunters also preferred large tinamous, but tinamous had high intrinsic rates of increase, short life span, and generation time. As a result, cracids and trumpeters were more susceptible to population decline from hunting and perhaps local extinction than species of the tinamous.

Management Recommendations

Few issues in the conservation community rival the intensity of the debate over sustainable use of wild species. One view is that sustainable use is an excuse to exploit wild species, while the other extreme advocates that sustainable use ensures conservation

of resources (IUCN et al 1996). Support for the sustainable use approach is becoming more and more evident in view of the failure of protectionist policies advocated by northern-based environmental institutions. The argument is that protectionist policies do not recognize the reality of wildlife use by communities in developing countries (Allen and Edwards 1995). As a result, problems between protectionist wildlife policies and the rural poor are becoming common place.

Sustainable use of wildlife could potentially be a tool for conservation (IUCN et al 1991). However, sustainable use requires knowledge on the biological and socio-economic factors that characterize the use of wild species. This study described the impact of hunting and the proximate factors that influence population decline from hunting. Species can be categorized as less vulnerable to hunting because of their adaptability to anthropogenic changes in habitat, behavioral traits that makes them less exposed to hunting, high rates of r_{max} , short-lived individuals and short generation time. The six species of tinamous correspond to these characteristics. In contrast, species can be categorized as more vulnerable to hunting because of their lack of adaptability to anthropogenic changes in habitat, behavioral traits that make them more exposed to hunting, and low rates of r_{max} , long-lived individuals and long generation time. The large cracids *M. tuberosa*, *P. jacquacu*, *P. cumanensis* and the trumpeter *P. leucoptera* correspond to these characteristics.

The conservation of Amazonian diversity will more likely be successful if strategies operate within the traditional exploitation system of rural Amazonians. Hunting patterns of ribereño people include frequent searches for wildlife in the areas surrounding the human settlements (short trips), generally to procure meat for the day's

meal, and less frequent searches on grounds away from the human settlements (long trips) generally to procure larger wildlife. Given the socio-economic realities of rural Amazonians, it is unlikely that they will refrain from shooting large birds that are easy to procure. A strategy that considers both socio-economic and biological factors may help conserve Amazonian birds.

This strategy includes the concept of functional refuge (McCullough 1987, Joshi and Gadgil 1991). A functional refuge is defined as the area or circumstance that protect the residual population from being hunted to extinction. Functional refugia include spatial attributes such as distant areas or habitat of difficult access, as well as, human aspects such as lack of motivation to access those areas (McCullough 1987). Behavioral and biological attributes of Amazonian birds suggest that a functional refuge for the tinamous can be realized "in situ", while a functional refuge for large cracids and trumpeters will need to set aside areas distant from the villages and free from permanent settlement. The influence of refugia on population responses is illustrated in Figure (6-1).

Population sizes within the shaded area represent potential functional refugia (McCullough 1987). Low abundance among the tinamous would represent a functional refuge because of the tinamous' secretive habits, and efficient antipredator behavior that would discourage hunters from attempting to procure individuals once detecting and procuring individuals becomes difficult. However, low abundance among the cracids and trumpeters near the settlements would not constitute a functional refuge because the ease of detection and hunting among these species would not prevent further decline to local extinction.

Areas distant from the villages were less frequented by hunters, and population abundances were closer to the species carrying capacity. This suggests that maintaining

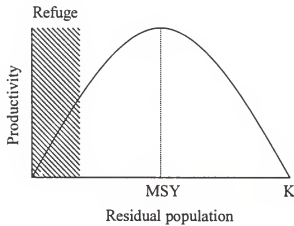


Figure 6-1. Representation of a hypothetical functional refuge. Population sizes within the shaded area constitute a refuge for species whose hunting becomes difficult at low densities discouraging hunters from hunting the population to extinction. Extracted from (McCullough 1987).

these areas free from permanent settlement are likely to maintain the population status observed. While distant areas may represent refugia, they are likely to function as a conservation strategy for Amazonian birds to the extent that better economic choices remain available. Results indicated that birds are generally a second choice relative to mammals. However, if mammalian wildlife is overhunted and becomes rare it is likely that hunting pressure shifts toward the more available and easy to procure species of birds. Hence, it is essential that management strategies encompass mammalian and avian wildlife to conserve both, as well as, the ecosystems in which they live in.

Differences in settlement patterns appear to have implications on determining the impact of hunting on Amazonian birds. Households distributed in larger areas are likely to have a lower impact than household concentrated around a central place using the same catchment areas. This pattern of settlement resembles those of native Amazonians intended to ensure the supply of wildlife for long terms (Ross 1978). This was also observed in the settlement in upland forest. Moreover, the planning of settlement pattern in a way that exert less impact on populations of wildlife could represent an alternative approach to promote sustainable use of wild birds in vast areas of forest controlled by groups of rural Amazonians (Stearman 1990).

The success of these recommendations will depend on the extent to which they involve local people in the management of their own resources (Townsend 1996, Fang et al 1997). Setting aside areas away from human settlements does not, by itself, guarantee the sustainable use and survival of large cracids and trumpeter. Hunting pressure in these areas need also be monitored. Because Peru's economic reality lacks financial resources to implement monitoring programs at the regional and national level, the involvement of local people could help with the monitoring of their own resources. This alternative is being implemented in the village of SP and can potentially represent an option toward the use and conservation of Amazonian birds.

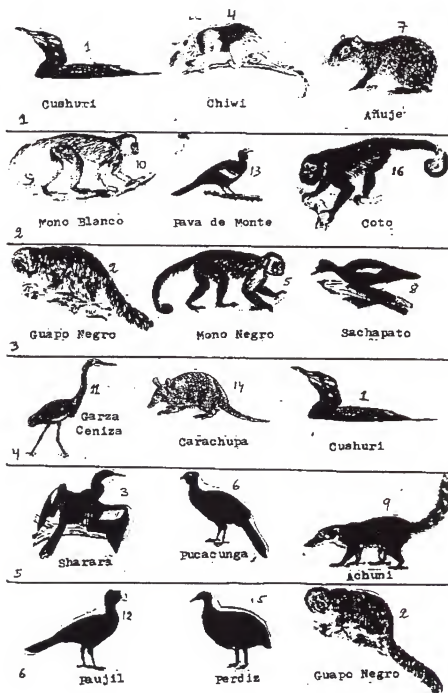
HUNTING DATA FORM

[illegible][illegible]

Fecha	Cuantos	Donde
15-2	2	La Alameda
03-4	2	La Alameda
26-4	1	La Alameda
11-5	1	Tamayo

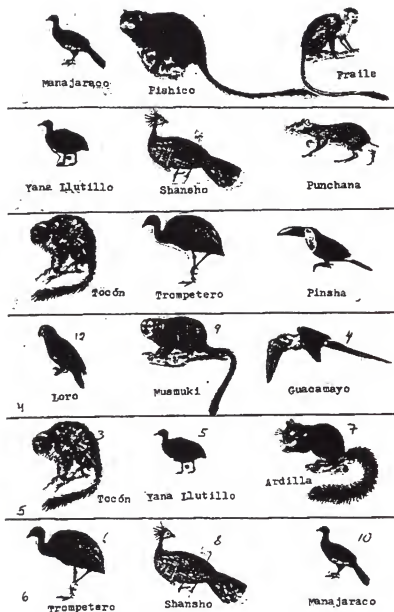
APPENDIX B

SAMPLE TRIADS OF THE LARGE-SIZED WILDLIFE CATEGORY



APPENDIX C

SAMPLE TRIADS OF THE SMALL-SIZED WILDLIFE CATEGORY



APPENDIX D

POPULATION DENSITY (INDIVIDUALS/KM²) OF SPECIES IN UPLAND FOREST USING THE PROGRAM DISTANCE^a.

	Unhunted – Upland forest				Hunted – Upland forest			
	Density (ind./km ²)	%CV	Df	95% Confid. interval	Density (ind./km ²)	%CV	Df	95% Confid. interval
<i>Tinamus gutattus</i>	3.2	46.6	12	1.2 - 8.4	6.7	18.3	58	4.5 - 9.4
<i>Tinamus major</i>	9.7	18.7	78	6.7 - 14	8.1	16.3	77	5.8 - 11.2
<i>Crypturellus variegatus</i>	4.9	43	5	1.6 - 14.4	3.4	24	28	2.1 - 5.7
<i>Crypturellus bartletti</i>	3.6	25	10	2.2 - 6.6	2.5	42	14	1.1 - 5.9
<i>Mitu tuberosa</i>	1.4	29.4	14	0.7 - 2.5	0.6	36	9	0.26 - 1.31
<i>Penelope jacquacu</i>	12.4	12.2	78	6.3 - 25.5	6.9	20	147	4.7 - 10.1
<i>Pipile cumanensis</i>	3.2	62	7	0.5 - 8.6	0.4	45	9	0.1 - 1
<i>Ortalis gutatta</i>	0.6	70.7	2	0.01 - 9.4	0.27	50	7	0.09 - 0.84
<i>Odontophorus stellatus</i>	7.2	56.4	9	2.2 - 23.7	7.6	53.3	3	1.4 - 37.3
<i>Cairina moschata</i> *	0.9				0.5			
<i>Phalacrocorax olivaceus</i> *	0.4				0			
<i>Ramphastos spp</i>	14.5	28.4	13	7.9 - 26.6	13.1	28.4	26	7.4 - 23.3
<i>Amazona spp</i>	6.4	34	20	3.2 - 12	5	35.3	9	2.1 - 9.9
<i>Ara spp</i>	14	30	34	7.7 - 25.2	5.13	40.4	10	2.15 - 12.2
<i>Leptotila rufaxila</i>	15.5	51.1	51	4.2 - 28.5	18.8	72	64	10.4 - 23
<i>Psophia leucoptera</i>	17.7	29.6	20	9.6 - 32.4	9.45	27	77	5.8 - 11.2
<i>Angintha aninga</i> *	0.77				1.5			
<i>Ardea cocoi</i> *	3.65				5.5			
<i>Cochlearius cochlearius</i> *	0.6				1			

* Density obtained using the method of variable transect length (Overton 1971).

^a Program "Distance" (Buckland et al. 1993).

APPENDIX E

POPULATION DENSITY (INDIVIDUALS/KM²) OF SPECIES IN VARZEA FOREST USING THE PROGRAM DISTANCE^a

	Varzea forest - unhunted				Varzea forest - Hunted			
	Density (ind./km ²)	%CV	Df	95% Confid. interval	Density (ind./km ²)	%CV	Df	95% Confid. interval
<i>Tinamus major</i>	10.7	14	69	8.1 - 14.2	7.3	19.1	11	4.8 - 11
<i>Crypturellus undulatus</i>	6.3	21.7	7	4 - 10.5	5	27	11	2.6 - 8.4
<i>Crypturellus cinereus</i>	4.94	30.1	13	2.6 - 9.3	8.5	34	17	4.4 - 16.5
<i>Mitu tuberosa</i>	2.4	15.4	14	1.7 - 3.3	2.2	35.3	10	1 - 4.7
<i>Penelope jacquacu</i>	5.7	28.7	23	3.1 - 10.4	3.15	23	25	2 - 5
<i>Pipile cumanensis</i>	6.43	27	14	3.6 - 11.4	10.7	21	23	7 - 16.5
<i>Ortalis gutatta</i>	0.51	64.5	2	0.03 - 6.4	3.2	55	8	1 - 10
<i>Odontophorus stellatus</i>	14	30.6	13	7.4 - 26.8	4.6	71	3	0.6 - 35.2
<i>Cairina moschata</i> *	2.54				0.55			
<i>Phalacrocorax olivaceus</i> *	7.26				3.3			
<i>Ramphastos spp</i>	5.1	54	11	1.6 - 15.4	7.4	58	5	1.8 - 29.6
<i>Amazona spp</i>	7.1	54	7	2.1 - 23	6.3	61	5	1.4 - 27
<i>Ara spp</i>	7.7	57.1	6	2.2 - 28.3	3.4	67.1	3	0.5 - 25
<i>Leptotila rufaxila</i>	15.5	18.3	64	10.2 - 22.2	18.8	15	14	13.7 - 26
<i>Psophia leucoptera</i>	13.2	28.4	30	7.5 - 23.3	0.6 *			
<i>Angintha aninga</i> *	5.71				8.24			
<i>Ardea cocoi</i> *	15				18.7			
<i>Cochlearius cochlearius</i> *	6.7				5.5			

* Density obtained using the method of variable transect length (Overton 1971).

^a Program "Distance" (Buckland et al. 1993).

REFERENCES

- Abrams, P. 1990. The evolution of anti-predator traits in prey in response to evolutionary change in predators. *Oikos* 59(2):147-156.
- Allen, C., S. Edwards. 1994. The sustainable use debate: Observations from the IUCN. *Oryx* 29(2):92-98.
- Alvard, M. 1995. Shotguns and sustainable hunting in the neotropics. *Oryx* 29(1):58-66.
- Alvard, M., J. Robinson, K. Redford, H. Kaplan. 1997. The sustainability of subsistence hunting in the neotropics. *Conservation Biology* 11(4):977-982
- Angermeier, P. 1994. Ecological attributes of extinction-prone species: Loss of freshwater fishes in virginia. *Conservation Biology* 9:143-158.
- Arango, R. 1992. Situación territorial y tratamiento legal de las areas indigenas del litoral Pacifico y de la Amazonia de Colombia. pp. 223-259. En *Derechos Territoriales Indigenas y Ecologia en la Selvas tropicales de America*, Fundacion GAIA and CEREC, eds. Bogota: GAIA/CEREC.
- Arita, H., J. Robinson, K. Redford. 1990. Rarity in Neotropical forest mammals and its ecological correlates. *Conservation Biology* 4(2):181-192.
- Atkinson, I. 1989. Introduced animals and extinctions. Pp 54-69 in *Conservation for the twenty-first century*, D. Western and M. C. Pearl, eds., Oxford: University Press.
- Ayres, J. M., and C. Ayres. 1979. Aspectos da caça no alto rio Aripuaná. *Acta Amazonica* 9(2):287-298.
- Ayres, J. M., D. Magalhaes-Lima, E. De Sousa Martins, J. L. Barreiros. 1991. On the track of the road: Changes in subsistence hunting in a brazilian amazonian village. Pp. 82-92 in *Neotropical Wildlife Use and Conservation*. J. G. Robinson and K. H. Redford eds., Chicago: University of Chicago Press.
- Ayres, J. M. 1993. As matas de várzea do Mamirauá. MCT-CNPq-Programa do Trópico Úmido, Sociedade Civil Mamirauá.
- Balee, W. 1985. Ka'apor ritual hunting. *Human Ecology* 13(4):485-510.

- Balee, W. 1989. The culture of amazonian forests. *Advances in Economic Botany* 7:1-12.
- Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution* 11(5):193-196.
- Balmford, A., M. Turyaho. 1992. Predation risk and lek-breeding in uganda kob. *Animal Behavior* 44(1):117-127.
- Balslev, H., L. J. Luteyn, B. Ollgard, L. B. Holm-Nielsen. 1987. Composition and structure of adjacent unflooded and floodplain forest in amazonian ecuador. *Opera Botanica* 92:37-57.
- Banse, K., S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs* 50:355-379.
- Basso, E. B. 1973. *The Kalapalo indians of central brazil*. New York: Holt Rinchart and Winston.
- Bayley, P., P. Vazquez, F. Ghersi, P. Soini, M. Pinedo. 1992. Estudio de impacto ambiental del proyecto Pacaya-Samiria, Loreto-Peru. The Nature Conservancy.
- Begazo, A. J. 1997. Use de la poblaciones de paujiles, pucacungas, pavas de monte y manajaracos (Cracidae-Galliformes) en el noreste peruano. Pp 257-266 in *Manejo de fauna silvestre en la Amazonia*. (T. G. Fang, R. E. Bodmer, R. Aquino, M. H. Valqui, eds.). La Paz: OFAVIM.
- Begazo, A. J., R. E. Bodmer. 1998. Use and conservation of the Cracidae (Aves-Galliformes) in the Perubian Amazon. *Oryx* 32(4):301-309.
- Begon, M., J. Harper., C. Townsend. 1990. *Ecology. Individuals, Populations and Communities*. Boston: Blackwell Scientific.
- Bendayán, N. 1990. Influencia socio-economica de la Fauna Silvestre en Iquitos. Tesis de Licenciatura. Loreto: Universidad Nacional de la Amazonia Peruana.
- Bengston, S. 1984. Breeding ecology and extinction of the great auk (*Pinguinus impennis*): anecdotal evidence and conjectures. *Auk* 101(1):1-12.
- Bernard, R. H. 1994. *Research methods in anthropology: Qualitative and quantitative approaches*. 2nd ed. Thousand Oaks, CA: Sage.
- Bibby, J. N., D. Burgess, A. Hill. 1992. *Bird census techniques*. London: Academic Press.

- Blake, J. B., A. Loiselle, T. C. Moermond, D. J. Levey, J. S. Denslow. 1990. Quantifying abundance of fruit for birds in tropical habitats. Pp 73-79 in *Avian foraging: Theory, methodology and applications*. M. L. Morrison, C. J. Ralph, C. J. Ralph, J. Verner, and J. R. Jehl, jr., eds. *Studies in Avian Biology* 13. Proceedings of an International Symposium of the Cooper Ornithological Society. Asilomar, CA.
- Blake, J. B., B. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk* 108(1):114-130.
- Bodmer, R. E. 1990. Responses of ungulates to seasonal inundation in the amazon floodplain. *Biological Conservation* 45(4): 303-310.
- Bodmer, R. E., T. G. Fang, L. Moya, R. Gill. 1994. Managing wildlife to conserve Amazonian forest: population biology and economic considerations of game hunting. *Biological Conservation* 67:29-35.
- Bodmer, R. E. 1995a. Susceptibility of Mammals to Overhunting in Amazonia. in Pp 292-295 in *Integrating People and Wildlife for a Sustainable Future*. Bissonette, J.A., and P. R. Krausman. eds., *Proceedings of the International Wildlife Management Congress*. Bethesda, MD: The Wildlife Society.
- Bodmer, R. E. 1995b. Managing Amazonian wildlife: Biological correlates of game choice by detribalized hunters. *Ecological Applications* 5:872-877.
- Bodmer, R. E., J. Eisenberg, K. Redford. 1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* 11(2):460-466.
- Bodmer, R. E., J. Penn, P. Puertas, L. Moya, T. Fang. 1997. Linking Conservation and local people through sustainable use of natural resources. in *Harvesting wild species: Implication for biodiversity conservation*, C. Freese, ed. Baltimore: Johns Hopkins University Press.
- Bodmer, R. E. (In Press). Sustainable use of Amazonian Mammals: Implications for community-based Protected Areas. in Dunestone and A. Entwistle eds., *Has the Panda had its Day: Future Priorities for the Conservation of Mammalian Biodiversity* London: Chapman & Hall.
- Bodmer, R. E., P. Puertas, J. Garcia, D. Diaz, C. Reyes. (In Press). Game Animals, Palms and People of the flooded forest: Management considerations for the Pacaya Samiria National Reserve, Peru. *Advances in Economic Botany*.
- Brack, A. 1990. Manejo integral de los Ecosistemas Amazonicos. Reunion Internacional, Experiencias para el desarrollo sostenido de la Amazoni. 20-24 de Agosto de 1990. Lima: Ediagraria.

- Brewer, R., L. Swander. 1977. Life history factors affecting the intrinsic rate of natural increase of birds of the deciduous forest biome. *Wilson Bulletin* 89(2):211-232.
- Bucher, E. H. 1992. The causes of extinction of the Passenger Pigeon. *Current Ornithology* 9:1-36.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake. 1993. Distance Sampling. Estimating the Abundance of Biological Populations. London: Chapman and Hall.
- Cajal, J. L. 1988. The lesser rhea in the Argentine puna region: Present situation. *Biological Conservation* 45:81-91.
- Castro, R. 1991. Behavioral ecology of two coexisting tamarin species (*Saguinus fuscicollis nigrifrons* and *Saguinus mytax mytax*).
- Caughley, G. 1977. Analysis of Vertebrate Populations. London : John Wiley & Sons, New York, 243 p.
- Caughley, G., A. Gunn. 1996. Conservation Biology in Theory and Practice. Boston: Blackwell Scientific.
- Cody, M. L. 1971. Ecological aspects of reproduction. Pp.461-178 in D. S. Farner and J. R. King, eds., *Avian Biology* Vol. 1. New York: Academic Press,
- Coimbra-Filho, C. 1971. Three forms of avifauna of northeastern Brazil threatened with extinction. *Revista Brasileira de Biologia* 31(2)239-247.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103-137.
- Coltrane, J. A. 1998. Impact of hunting on primate populations in the Peruvian Amazon. Master Thesis. Department of Wildlife Ecology and Conservation. University of Florida, Gainesville.
- Cook, J. G., T. Stutzman, C. Bowers, K. Brenner, L. Irwin. 1995. Spherical densiometer produce biased estimates of forest canopy cover. *Wildlife Society Bulletin* 23(4):711-717.
- Cook, T. D., D. T. Campbell. 1979. Quasi-experimentation: Design and analysis issues for field settings. Chicago: Rand McNally College Publication.
- Coomes, O. T. 1992. Blackwater rivers, adaptation and environmental heterogeneity in Amazonia. *American Anthropologist* 94(3): 698-701.

- Cox, G. 1997. Cracidae country report for Bolivia. Pp 474-481. in *The Cracidae: Their biology and conservation*. Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, F. Olmos, eds., Toronto: Hancock House.
- Cracid Taxon Advisory Group. 1994. III International Cracid Symposium. Houston, TX: Houston Zoological Garden. Houston Texas.
- Cullen, L. 1997. Hunting and biodiversity in Atlantic Forest fragments, Sao Paulo, Brazil. University of Florida, Master's Thesis. 134 Pp.
- Defler, S., T. Defler. 1997. Anotaciones sobre los los Cracidos del bajo Apapornis en el Sureste de Colombia. Pp 289-287. in *The Cracidae: Their biology and conservation*. Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Toronto: Hancock House Publisher.
- Delacour, J., D. Amadon. 1973. *Curassows and Related Allies*. New York: The American Museum of Natural History.
- Denevan, W., J. M. Treacy, J. B. Alcorn, C. Padoch, J. Denslow, S. Flores Paitan. 1984. Indigenous agroforestry in the Peruvian Amazon: Bora indians managements of swidden fallows. *Interciencia* 9(6):346-357.
- Denslow, J., T. Moermond, D. Levey. 1986. Spatial components of fruit display in understory trees and shrubs. Pp 37-44 in *Frugivory and seed dispersal*. A. Estrada, and T. Fleming, eds., Dordrecht, Boston: W. Junk, Hingham, MA.
- Devore, I., K. Hall. 1965. Baboon ecology. in *Primate behavior: Field studies on monkey and apes*. I. Devore ed., New York: Holt, Rinehart, Winston.
- Dobson, A., E. Ortiz. 1988. "Going going...guan!" *Trends in Ecology and Evolution* 9:217-218.
- Dourojeanni, M. J. 1985. Over-exploited and under-used animals in the Amazon region. Pp 419-422 in *Key environments: Amazonia*. G. T. Prance and T. E. Lovejoy, eds., New York: Pergamon Press.
- Dourojeanni, M. 1990. *Amazonia, Que hacer? Iquitos: Centro de Estudios Teológicos de la Amazonia*.
- Ducey, P., E. Brodie. 1991. Evolution of antipredator behavior: Individual and population variation in a Neotropical Salamander. *Herpetologica* 47(1):89-95.
- Dufour, D. L. 1990. Use of tropical rainforest by native Amazonians. *BioScience* 40(9):652-659.

- Dumont, J. F., S. Lamotte, F. Kahn. 1990. Wetland and upland forest ecosystems in peruvian amazonia: Plant species diversity in the light of some biological and botanical evidence. *Forest Ecology and Management* 33(34): 125-139.
- Dunning, J. B. 1992. CRC handbook of avian body masses. CRC Boca Raton, Florida.
- Egoavil, E. O. 1992. Perfil demografico de la region Loreto. Iquitos Peru: Instituto de Investigaciones de la Amazonia Peruana.
- Eisenberg, J., F. O'Connell, P. August. 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. Pp 187-207 in *Vertebrate ecology in northern Neotropics*, J. F. Eisenberg ed., Smithsonian Institute Press, Washington, DC.
- Emmons, L. 1984. Geographic variation in densities and diversities of non-flying mammals in amazonia. *Biotropica* 16(3):210-222.
- Encarnación, F. 1993. El bosque y las formaciones vegetales en la llanura amazónica del Peru. *Alma Mater* 6:95-114.
- Estudillo-Lopez, J. 1988. Breeding Cracids in Captivity. Pp. 159-163 in *Proceedings of World Conference of Breeding of Endangered Species in Captivity*, No 5.
- Euler, C. 1900. Descrição de ninhos e ovos das aves do Brasil. *Revista do Museo Paulista* 4:9-148.
- Fang, T., R. Bodmer, R. Aquino, M. Valqui. 1997. Manejo de Fauna Silvestre en la Amazonia. United Nations Development Program/Global Environmental Facility/University of Florida. La Paz Bolivia.
- Fitzgibbon, C. D., H. Mogaka, J. H. Fanshawe. 1996. Subsistence hunting in Arabuko-Sokoke forest, Kenya, and its effects on mammal populations. *Conservation Biology* 9: 1116-1126.
- Fitzpatrick, J. W. 1985. Form, foraging behavior, and adaptive radiation in the Tyrannidae. *Ornithological Monographs* 36:447-470.
- Fodgen, M. P. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114:307-343.
- Forshaw, J. 1973. *Parrots of the world*. Melbourne: Lansdowne Press, p. 584.
- Forti, M. T., C. Vispo. In Press. Estimación del área de vivienda de la gallina de monte *Tinamus major* en la cuenca del río caura, estado Bolívar, Venezuela.

- Franco, A., M. Santamaría. 1997. Biología reproductiva del Paujil (*Mitu salvini*). Pp 423-424. in *The Cracidae: Their biology and conservation*, Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Hancock House Publisher.
- Freese, A. H. 1997. The "use it or loose it debate": Issues of conservation paradox. Pp 1-48. in *Harvesting wild species: Implications for biodiversity conservation*. C. H. Freese ed., Baltimore: John Hopkins University Press.
- (FPCN), Fundación Peruana para la Conservación de la Naturaleza. 1994. Estudio socio-económico de las poblaciones vecinas a la Reserva Nacional Pacaya-Samiria. Informae Fase I. Iquitos: FPCN, 37p.
- Furch, K. 1984. Water chemistry of the amazon basin: The distribution of chemical elements among freshwaters. Pp 167-199 in *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin*. H. Sioli, ed., Dordrecht, Boston: W. Junk, Hingham, MA.
- Garber, P. A. 1993. Seasonal patterns of diet and ranging in two species of Tamarin monkeys: Stability versus variability. *Journal of Primatology* 14(1):145-166.
- Gaviria, A. 1981. La fauna silvestre y su aprovechamiento por las comunidades campesinas del río Pichis. *Revista Forestal del Perú*.
- Gentry, A. H. 1988. Tree species richness of upper Amazonian forest. *Proceedings of the National Academy of Sciences* 84:156-159.
- Gentry, A. H. 1992. Tropical forest diversity: Distributional pattern and their conservational significance. *Oikos* 63:19-28.
- Gilbert, L. 1980. Food web organization and the conservation of Neotropical Diversity. Pp 11-33 in *Conservation Biology*, M. E. Soulé, B. A. Wilcox, eds., Sinauer Sunderland, MA.
- Gill, F. B. 1990. *Ornithology*. New York: W. H. Freeman.
- Glanz, W. 1991. Mammalian densities at protected versus hunted sites in central Panama. Pp 163-173 in *Neotropical Wildlife Use and Conservation*. J. G. Robinson and K. H. Redford eds., Chicago: University of Chicago Press.
- Gonzales, G. 1998. Importancia socio-económica de las aves silvestres para los pobladores del sector meridional de la Reserva Nacional Pacaya-Samiria. Tesis de Maestría del Programa de Conservación y Manejo de Fauna. Universidad Agraria "La Molina".
- Gotelli, N. J. 1995. *A Primer of Ecology*. Sunderland Sinauer. MA.

- Goulding, M. 1980. *The Fishes and the Forest, exploration in Amazonian Natural History*. Berkeley: University of California Press.
- Greenfield, P., F. Ortiz-Crespo. 1997. An update of the distribution and status of Ecuadorian Cracids. PP 314-319. in *The Cracidae: Their biology and conservation*. Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.
- Gross, D. 1975. Protein capture and cultural development in the amazon basin. *American Anthropologist* 77:526-549.
- Gutierrez, R. 1997. Observaciones de la población de *Mitu tuberosa* (Linneus, 1776) en el Parque Nacional del Manu, Perú. Pp 80-87. in *The Cracidae: Their biology and conservation*., Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.
- Hames, R. 1989. A comparison of the efficiencies of the shotgun and the bow in neotropical forest hunting. *Human Ecology* 7(3):219-252.
- Hancock, J., M. Kushlan. 1984. *The Herons Handbook*. New York: Harper & Row.
- Hawkes, K., J. O'Connel, L. Rogers. 1997. The behavioral ecology of modern hunter-gatherer, and human evolution. *Trends in Ecology and Evolution* 112(1)29-31.
- Henneman, W. 1983. Relationship among body mass, metabolic rate and intrinsic rate of natural increase in mammals. *Oecologia* 56:104-108.
- Hill, K., K. Hawkes. 1983. Neotropical hunting among the Ache of eastern Paraguay. Pp 139-188. in *Adaptive responses of native Amazonians*, R. B. Hames and W. T. Vickers, eds., New: Academic Press 516 pp.
- Hilty, S. 1994. *Birds of tropical America: a watcher introduction to behavior, breeding and diversity*. Chapters Canada. P. 304.
- Hilty, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12:292-306.
- Hilty, S., L. Brown. 1986. *A guide to the birds of Colombia*. Princeton: Princeton University Press.
- Hollander, M. D., D. Wolfe. 1999. *Non-parametric statistical methods*. 2nd ed. New York: John Wiley.
- Howe, H. 1983. Annual variation in a Neotropical seed-dispersal system. *British Ecological Society. Special. Publications No. 2*. p. 211-228. 1983.

- Hubbell, S. P., R. S. Foster. 1986. Diversity in canopy trees in tropical forests and implications for conservation. Pp 234-252 in Tropical Rain forest : Ecology and Management, S. L. Sutton, T. C. Whitmore, A. C. Chadwick, eds., Oxford: Blackwell Scientific.
- Hueck, K. 1978. Los bosques de Sudamerica. Ecologia Composicion e importancia económica. Cooperacion Tecnica Alemana (GTZ). Lima, Peru: Documento de Trabajo.
- Hurtado, A. M., K. Hawkes, K. Hill, H. Kaplan. 1985. Female subsistence strategies among aché hunter-gatherers of eastern Paraguay. Human Ecology 13(1):1-28.
- Idrisi, 1997. Idrisi for windows version 2.0. Clark labs for cartographic technology and geographic analysis. Clark University. Worcester: MA.
- Inigo-Elias, E. E., M. A. Ramos. 1991. The psittacidae trade in Mexico. Pp. 380-392 in Neotropical Wildlife Use and Conservation, J. G. Robinson and K. H. eds., Chicago: University of Chicago Press.
- IUCN, Species Survival Commission. 1996. IUCN Red list categories. IUCN, Gland, Switzerland.
- IUCN/UNEP/WWF. 1991. Caring for the earth. A strategy for sustainable development. IUCN/UNEP/WWF, Gland, Switzerland.
- Janson, C. H. 1983. Adaptation of fruit morphology to dispersal agents in Neotropical rain forest. Science 219:187-189.
- Janson, C. H. 1992. Social correlates of individual spatial choice in foraging groups of Brown capuchins *Cebus apella*. Animal Behavior 40(5):910-921.
- Janzen, D. 1974. Tropical blackwaters, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6:69-103.
- Johnsgard, P. 1978. Ducks, Geese, and Swans of the world. Lincoln: University of Nebraska Press.
- Jorgenson, J. P. 1993. Gardens, wildlife densities, and subsistence hunting by Maya indians in Quintana Roo, Mexico. Doctoral dissertation, Univeristy of Florida, Gainesville.
- Joshi, N., M. Gadgil. 1991. On the role of refugia in promoting prudent use of biological resources. Theoretical Population 40:211-229.

- Kalliola, R., M. Puhakka. 1993. Geografia de la selva baja peruana. Pp 9-22 in Amazonia Peruana, vegetacion humeda tropical en el llano subandino, Kalliola, R., Puhakka, M., and W. Danjoy, eds., Lima: Proyecto Amazonia, Universidad de Turku-Ofician Nacional de Evaluacion de Recursos Naturales.
- Kalliola, R., M. Puhakka, W. Danjoy. 1993. Amazonia Peruana. Vegetacion humeda tropical en el llano Subandino. Proyecto Amazonia, Universidad de Turku-Ofician Nacional de Evaluacion de Recursos Naturales.
- Kapos, V., E. Pellant, A. Bien, J. Freskos. 1990. Gap frequency in lowland rainforests sites on contrasting soils in Amazonian Ecuador. *Biotropica* 22(3):218-225.
- Karr, J. 1990. Avian survival rate and the extinction process in Barro Colorado Island, Panama. *Conservation Biology* 4:391-397.
- Kelley, K. 1993. Recaptures and longevity records. *North American Bird Bander* 18(1):39-40.
- Klinge, H., W. J. Junk, C. I. Revilla. 1990. Status and distribution of forested wetlands in tropical South America. *Forest Ecology and Management* 33/34:81-101.
- Kotler, J., R. Brown, W. Smith, J. Wirtz. 1988. The effect of morphology and body size on rates of owl predation on desert rodents. *Oikos* 53:145-152.
- Laake, J. L., S. T. Buckland, D. R. Anderson, K. P. Burnham. 1994. Distance user's guide V2.1. Colorado Cooperative Fish and Wildlife Research Unit. Fort Collins: Colorado State University.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2:314-320.
- Leopold, A. S. 1959 *Wildlife of Mexico the game birds and mammals*. Berkeley : University of California Press.
- Levey, D. 1988. Tropical wet forest tree-fall gaps and distributions of understory birds and plants. *Ecology* 69(4):1076-1089.
- Levey, D. J., F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: Resource availability and movement patterns in Neotropical birds. *American Naturalists* 140(3):447-476.
- Levey, D., T. Moermond, J. Denslow. 1994. Frugivory: An overview. Pp 282-394 in *La Selva: Ecology, and natural history of a neotropical rain forest*, L. A. McDade, K.

- S.Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds., University of Chicago Press, Chicago, IL.
- Lindstedt, S., W. Calder. 1976. Body size and longevity in birds. *Condor* 78(1):91-94.
- Loiselle, B., J. Blake. 1991. Temporal variation in birds and fruit along an elevational gradient in Costa Rica. *Ecology* 72(1):180-193.
- Loiselle, B., J. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a Neotropical lowland wet forest. *Vegetatio* 107-108:117-189.
- Lotka, J. 1925. *The Elements of Physical Biology*. Baltimore: Williams and Wilkins.
- Lovejoy, T. E., A. R. Brash. 1984. Homage au Jean D'arc or the Conservation of the Cracidae. *Dodo New Jersey Wildlife Preservation Trust* 21:33-42.
- Madge, S., H. Burn. 1988. *Waterfowl. An identification guide to the ducks, geese and swans of the world*. Boston: Houghton Mifflin.
- Malleux, J. 1975. *Mapa Forestal del Peru. Memoria explicativa*. Lima: Universidad Nacional Agraria La Molina.
- Marengo, O. J. 1984. Estudio sinoptico-climatico de la los friajes en la Amazonia Peruana. *Revista Forestal de Peru*. XII (1-2):55-80.
- Marez, C. 1992. Brazil, Amazonia e Indios: El derecho del jaque. Pp 75-90 en *Derechos Territoriales Indigenas y Ecología en la Selvas tropicales de America*, Fundación GAIA and CEREC, eds., Bogota: GAIA/CEREC.
- Marion, W., F. Raymond. 1978. Nesting ecology of the plain chachalaca in south Texas. *Willson Bulletin* 90(3):386-395.
- Martin, T. 1996. Life history evolution in tropical and south temperate birds: What do we really know?. *Journal of Avian Biology* 27(4):263-272.
- May, R. 1974. Ecosystem patterns in randomly fluctuating environments. *Progress in theoretical biology*. 3:1-52.
- McCoullough, D. R. 1996. Spatially structured populations and harvest theory. *Journal of Wildlife Management* 60:1-9.
- McCullough, D. R. 1987. *The theory and management of Odocoileus populations*, in *Biology and management of the Cervidae*, C. Wemmer, ed., Washington DC: Smithsonian Press.

- Medina, G., L. Suarez, P. Mena. 1994. The Bearded Guan *Penelope barbata* in the Podocarpus National Park, Loja, Ecuador. The Cracid Newsletter, Volume 3, No 1. Pp 4-7.
- Milberg, P., T. Tyrberg. 1993. Naive birds and noble savages- A review of caused historic extinctions of island birds. *Ecography* 16(3):229-250.
- Mitchell, C., E. Racz-Luna. 1991. The impact of human hunting on primate and game bird populations in the Manu Biosphere Reserve in southeastern Peru. Report prepared for Wildlife Conservation International. New York Zoological Society, Bronx, NY.
- Mittermaier, H. R. 1982. Conservation of Primates in Surinam. *International Zoological Yearbook* 22:59-65.
- Munn, C. A. 1994. Macaws: Winged rainbows. *National Geographic* 185:118-140.
- Murray, B. 1992. The evolution of clutch size: A reply to Wootton, Young, and Winkler. *Evolution* 46(5):1581-1584.
- Nadkarni, N. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *American Zoologist* 34(1):70-78.
- Nichols, J., M. Haramis. 1980. Inferences regarding survival and recovery rates of winter-banded canvasbacks. *Journal of Wildlife Management* 44:164-173.
- Norconk, M. A. 1986. Interactions between primate species in the Neotropical forest: Mixed-species troops of *Saguinus myxax* and *Saguinus fuscicollis* (Callithrichidae). Doctoral Dissertation, University of California, Los Angeles.
- Novaro, A. 1995. Sustainable harvest of Culpeo fox in Patagonia. *Oryx* 29:18-22.
- Ojasti, J. 1993. Utilización de la fauna silvestre en America Latina. Situación y perspectivas para un manejo sostenible. *FAO Guía para la Conservación* No 25. Rome, Italy.
- Ollson, M. 1977. The captive propagation of the curassows (Cracidae). in: *Proceedings of the Regional Conference. International Zoological Yearbook. Parks and Aquariums.* pp 221-223.
- O'Neil, J. P. 1991. The Cracidae - An overview. *American Association of Zoos and Aquariums. Regional Conference.* pp. 221-223.
- Ortiz, E., J. O'Neil. 1997. Situación de la familia Cracidae en el Perú. Pp 361-374. in *The Cracidae: Their biology and conservation.* Strahl, S., S. Beaujon, D. Brooks,

- A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.
- Overton, S. 1971. Estimating the number of animals in wildlife populations. Pp. 403-457 in *Wildlife management techniques*, 3rd edition R. H. Giles. Washington, D.C.: The wildlife Society.
- Padoch, C. 1988. People of the floodplain forest. Pp 127-141. in *People of the tropical forest*. J. S. Denslow and C. Padoch, eds., Berkeley: University of California Press.
- Pastor, J. R. Moen, Y. Cohen. 1997. Spatial heterogeneity, carrying capacity, And feed-backs in animal-landscape interactions. *Journal of Mammalogy* 78(4):1040-1052.
- Peltonen, A., I. Hanski. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. *Ecology* 72:1698-1708.
- Perea, E. 1995. Política para el desarrollo y la conservación de la Amazonía. Amazonia: Desarrollo y tecnología. Primera conferencia. Cali-Colombia.
- Peres, C. A. 1990. Effects of hunting on western Amazonian primates communities. *Biological Conservation* 53:47-59.
- Peres, C. A. 1996a. Population status of white-lipped *Tayassu pecari*, and collared pecary *T. tajacu* in hunted and unhunted Amazonian forest. *Biological Conservation* 77: 115-123.
- Peres, C. A. 1996b. Effects of selective hunting and forest types on the structure of Amazonian primate communities. *Folia Primatologica* 67(2):107.
- Peres, C. A. 1997. Primate community structure at twenty Amazonian flooded and unflooded forest. *Journal of Tropical Biology* 13:381-405.
- Pierret, P., M. Dourojeanni. 1967. Importancia de la caza para la alimentación humana en el curso inferior del río Ucayali, Perú. *Revista Forestal del Perú*. 1(2):10-21.
- Pires, J. G. Prance. 1987. The vegetation types of Brazilian Amazon. Pp.109-143. in *Key Environments: Amazonia*, Prance G. T. and Lovejoy T., eds., Oxford: Pergamon Press. 442 p.
- Posey, D., J. Frechione, J. Eddins, L. Francelino Da Silva, with D. Mayers, D. Case, P. MacBeath. 1984. Ethnoecology as applied anthropology in Amazonian development. *Human Organization* 43(2):95-107.
- Prescott-Allen R., C. Prescott-Allen. 1982. What's wildlife worth? International institute for environmental and development, Washington, DC.

- Raez-Luna, E. F. 1995. Hunting large primates and conservation of the Neotropical Rain Forests. *Oryx* 29:43-48.
- Redford, K., J. Robinson. 1987. The game of choice: patterns of indian and colonists hunting in the Neotropics. *American Anthropologists* 89(3):650-667.
- Redford, K., A. Stearman. 1989. Local peoples and the Beni Biosphere Reserve, Bolivia. *Vida Silvestre Neotropical* 2(1):49-56.
- Redford, K. H., Robinson, J. G. 1991. Subsistence and commercial uses of wildlife in Latin America. Pp 6-23 in *Neotropical Wildlife Use and Conservation*, J.G. Robinson and K. H. Redford eds., Chicago: University of Chicago Press.
- Redford, K. 1992. The empty forest. *Bioscience* 42(6):412-426.
- Redford, K. H. Klein, C. Murcia. 1992. The incorporation of game animals into small scale agroforestry systems in the Neotropics. Pp 333-358 in *Conservation of Neotropical rain forest: Building traditional resource use*, K. H. Redford and C. Padoch, eds., New York: Columbia University Press.
- Reichel, J., T. Lemke. 1994. Ecology and extinction of the Mariana Mallard. *Journal of Wildlife Management*. 58(2):199-205.
- Reid, W. V., K. R. Miller. 1989. Keeping options alive: The scientific basis for conserving biodiversity. Washington, DC: World resources institute.
- Reid, W. V. 1992. How many species will there be? Pages 55-73 in *Tropical deforestation and species extinction*. T. C. Whitmore and J. A. Sayer, eds., London: Chapman & Hall.
- Ricklefs, R. E. 1983. Comparative avian demography. *Current Ornithology* 1:1-32.
- Robinson, J., K. Redford. 1986. Intrinsic rate of population increase in Neotropical forest mammals: relationship to phylogeny and diet. *American Naturalist* 128(5):665-680.
- Robinson, S., D. Wilcove. 1989. Conserving tropical raptors and game birds. *Conservation Biology* 3(2):192-193.
- Robinson, J. G., K. H. Redford. 1991. Sustainable harvest of Neotropical forest animals. Pp. 415-429 in *Neotropical Wildlife Use and Conservation*. J. G. Robinson and K. H. Redford, eds., Chicago: University of Chicago.

- Robinson, J. G. 1993. Community based approaches to wildlife conservation in Neotropical forests. Prepared for the Liz Claiborne and Art Foundation Community based conservation Workshop, Virginia, USA.
- Ross, C. 1992. Environmental correlates of the intrinsic rate natural increase in primates. *Oecologia* 90:383-390.
- Ross, E. B. 1978. Food taboos, diet, and hunting strategy: the adaptation to animals in Amazon cultural ecology. *Current Anthropology* 19(1):1-16.
- Ruddle, K. 1970. The hunting technology of maraca indians. *Anthropologica* 25:21-63.
- Safirio, J., R. Hames. 1983. The forest and the highway. Cultural survival report II. Cultural survival. Cambridge: MA.
- Saitre, R., J. Saitre. 1992. Causes of land bird extinctions of French Polynesia. *Oryx* 26(4):215-222.
- San Roman, J. V. 1975. Perfiles historicos de la Amazonia Peruana. Lima. Ediciones Paulinas. 240 p.
- Santamaria, M., M. F. Franco. 1996. Area vital, habitos alimenticios y otros aspectos de la historia natural del Paujil *Mitu salvinii* Pp. 267- 282 in Manejo de Fauna Silvestre en la Amazonia., T. G. Fang, R. E. Bodmer, R. Aquino y M. Valqui, eds., La Paz: Editorial Instituto de Ecologia.
- Saravia, J. A. 1992. Aprovechamiento de la fauna silvestre en Dantas. *Revista Forestal del Peru* 19(1), 127-134.
- Schifter, H. 1989. Early longevity and breeding records of curassows (Cracidae). *Rivista Italiana di Ornitologia* 59(2):70-74.
- Sermeño, A. 1997. Alimentación y reproducción del Paujil (*Crax rubra*) en El Salvador. Pp 71-78 in The Cracidae: Their biology and conservation., Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.
- Sieving, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology* 73(6): 2310-2328.
- Shaw, J. H. 1991. The outlook for sustainable harvest of wildlife in Latin America. Pp. 24-34 in Neotropical Wildlife Use and Conservation, J. G. Robinson and K. H. Redford eds., Chicago: University of Chicago Press.
- Sherman, P. T. 1995. Breeding biology of white-winged trumpeters (*Psophia leucoptera*) in Peru. *Auk* 112(2):285-295.

- Sick, H. 1993. *Birds in Brazil*. Princeton: Princeton University Press.
- Silva, J., S. Strahl. 1991. Human impact on populations of Chachalacas, Guans and Curassows (Galliformes:Cracidae) in Venezuela. Pp 37-52 in *Neotropical Wildlife Use and Conservation*, J. G. Robinson and K. H. Redford eds., Chicago: University of Chicago Press.
- Sioli, H. 1984. The Amazon. Pp 127-165 in *Limnology and landscape ecology of mighty tropical river and its basin*. H. Sioli ed., Dordrecht, Boston: W. Junk, Hingham, MA.
- Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* 36:575-594.
- Smith, N. 1976. Utilization of game along Brazil's transamazon highway. *Acta Amazónica* 6(4):455-466.
- Snow, D. 1981. Tropical frugivore birds and their food plants: a world survey. *Biotropica* 13:1-14.
- Soini, P. 1990. La avifauna de pacaya: Lista actualizada de especies y evaluacion preliminar de la abundancia y preferencia de habitat. Informe Pacaya No 31 (Corepasa, Iquitos, Peru), 13 p.
- Soulé, M. E. 1985. What is conservation biology? *BioScience* 35:727-734.
- SPSS, 1996. *Statistical Program for Social Sciences*. SPSS Inc. Boston, MA.
- Stanford, P. 1995. The influence of Chimpanzee predation on group size and antipredator behavior in Red Colobus monkeys. *Animal Behavior* 49(3):577-587
- Stattersfield, A. J., M. Crosby, A. J. Long, D. C. Wege. 1998. *Endemic bird areas of the world. Priorities for biodiversity conservation*. Cambridge: The Burlington Press.
- Stearman, A. M. 1990. The effects of settler incursion on fish and game resources of the Yuqui, a native Amazonian society of eastern Bolivia. *Human Organizations* 51(3):235-244.
- Stearman, A., K. Redford. 1993. Forest-dwelling native Amazonians and the Conservation of biodiversity: Interest in common or in collision? *Conservation biology* 7(2), 248-255.
- Stearman, A., K. Redford. 1995. Game management and cultural survival: The yuqui ethno-development project in lowland Bolivia. *Oryx* 29(1):29-34.

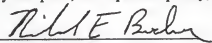
- Stotz, D.F., J. W. Fitzpatrick, T. A. Parker III, D. K. Moskovits. 1996 Neotropical birds, ecology and conservation. University of Chicago Press, Chicago and London.
- Strahl, S. D., A. Grajal. 1991. Conservation of large avian frugivores and the management of Neotropical protected areas. *Oryx* 25:50-55.
- Strahl, S., J. Silva. 1997. Census methods for Cracids. Pp 26-33 in *The Cracidae: Their biology and conservation*, Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.
- Sweede, K. 1998. Leaf litter and invertebrate biomass in the Neotropical forest. *Bulletin of the Ecological Society of America*. Vol. 74(Supplement 2:189).
- Tello, A., R. Pedraglio. 1997. Posibilidad de la crianza comercial de Cracids en Cautiverio, Pp 161-165. in *The Cracidae: Their biology and conservation*, Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.
- Temple, S. A. 1978. Endangered birds: Management techniques for preserving threatened species. University of Wisconsin Press, Madison, 466 p.
- Temple, S. A. 1986. The problem of avian extinctions. *Current Ornithology* 3:453- 485.
- Terborgh, J. W. 1974. Preservation of natural diversity: The problem of extinction prone species. *BioScience* 24:715-722.
- Terborgh, J. W., B. Winter. 1980. Some causes of extinction. Pp 119-133 in *Conservation biology and evolutionary ecological perspective*. M. E. Soulé and B. A. Wilcox, eds. Sunderland MA: Sinauer Associates.
- Terborgh, J. W. 1985. Habitat selection in Amazonian birds. Pp 311-338 in *Habitat selection in birds*, M. L. Cody, ed., Orlando: Academic Press.
- Terborgh, J. W. 1986. Keystone Plant Resources in the Tropical Forest. Pp 330-344 in *Conservation Biology*, M. E. Soule, ed., Sunderland, MA: Sinauer Associates.
- Terborgh, J. W., S. Robinson, T. Parker, C. Munn, N. Pierpoint. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60(2):213-238.
- Townsend, W. R. 1995. Living on the edge: Sirionó hunting and fishing in lowland Bolivia. Doctoral dissertation, Dpt. of Wildlife Ecology and Conservation. University of Florida, Gainesville.
- Vazquez, R., A. H. Gentry. 1989. Use and misuse of forest-harvested fruits in the Iquitos area. *Conservation Biology*. 3:350-361.

- Vickers, T. W. 1991. Hunting yields and game composition over ten years in an Amazonian indian territory. Pp. 53-81 in *Neotropical Wildlife Use and Conservation*, J. G. Robinson and K. H. Redford, eds., Chicago: University of Chicago Press.
- Vickers, W. T. 1980. An analysis of Amazonian hunting yields as a function of settlement age. Pp 7-29 in *Working Papers on South American Indians*, W. T. Vickers and K. M. Kensinger, eds., Bennington VT: Bennington College.
- Villarejo, A. 1988. *Asi es la selva*. Publicaciones CETA, Centro de Estudios Teologicos de la Amazonia. Iquitos, Peru. 330 p.
- Vitt, L., P. Zani. 1998. Ecological relationships among sympatric lizards in a transitional forest of the northern Amazon of Brazil. *Journal of Tropical Ecology* 14(1):63-86.
- Wheelwright, N. 1986. A seven-year study of individual variation of fruit production in tropical-bird dispersed tree species in the family Lauracea. Pp21-36 in *Frugivores and Seed Dispersal*, A. Estrada and T. Fleming, eds., Dordrecht, Boston: W. Junk, Hingham, MA.
- Whitesides, G. H., J. Oates, M. Green, R. Kluberanz. 1988. Estimating primate density from transects in a West African rainforest: A comparison of techniques. *Journal of Animal Ecology* 57:345-367.
- Whitmore, T. C., G. Prance. 1987. *Biogeography and quaternary history in Tropical America*. Oxford: Clarendon Press.
- Yost, J. R., P. M. Kelley. 1983. Shotguns, blowguns and spears: The analysis of the technological efficiency. Pp 189-224 in *Adaptive response of native Amazonians*, R. T. Hames and T. W. Vickers, eds., New York: Academic Press.
- Zent, S. 1997. *Piaroa and the Cracidae*. Game management under shifting cultivation. Pp 177-194. in *The Cracidae: Their biology and conservation*, Strahl, S., S. Beaujon, D. Brooks, A. Begazo, G. Sedaghatkish, and F. Olmos, eds., Washington: Hancock House Publisher.

BIOGRAPHICAL SKETCH

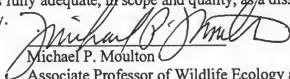
Alfredo Jaime Begazo was born March 13, 1963, in Arequipa Peru. He grew up in Lima, the capital city. From an early age he developed an appreciation for wildlife while living in a small coastal province in Southern Perú. His house was a zoo with all kinds of animals; birds dominated the landscape. Alfredo attended the Agrarian University, La Molina where he obtained an engineering degree in forestry in 1990. He worked for nearly a year in Manu National Park in Peru, where he became involved with issues of avian conservation in the Neotropics. In 1990 he obtained a fellowship to attend a field ornithology-training program in Massachusetts and Puerto Rico. This period was followed by an internship at Archbold Biological Station in Florida. Alfredo started graduate work at the University of Florida in the fall of 1992, received a Master of Science degree in Wildlife Ecology and Conservation in the spring of 1995 and Ph. D. in Wildlife Ecology and Conservation in August 1999.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Richard E. Bodmer, Chair
Assistant Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



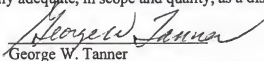
Michael P. Moulton
Associate Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



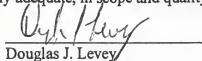
Kathryn E. Sieving
Assistant Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



George W. Tanner
Professor of Wildlife Ecology and Conservation

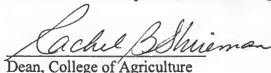
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Douglas J. Levey
Professor of Zoology

This dissertation to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1999



Dean, College of Agriculture

Dean, Graduate School

LD
1780
1999
B476

UNIVERSITY OF FLORIDA



3 1262 08554 3006